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PHYLOGENETIC RELATIONSHIPS OF THE GENUS *PIPTOCHAETIUM* (POACEAE, POOIDEAE, STIPEAE): EVIDENCE FROM MORPHOLOGICAL DATA[1]

Ana María Cialdella[2] *and*
Liliana Mónica Giussani[2]

ABSTRACT

A systematic treatment of the entire genus *Piptochaetium*, which complements that of Cialdella and Arriaga for the South American species, is presented herein. A synopsis of 36 species and 2 varieties, a key to identify these species, as well as synonymy and geographical distribution, are given. Illustrations and photographs of diagnostic characters are presented for the North American species for the first time. We propose a phylogenetic hypothesis for the genus based on morphological and anatomical characters. Monophyly of *Piptochaetium* was supported by the combination of three synapomorphies: a grooved palea, involute lemma margins that fit into a longitudinal palea groove, and the palea protruding from the lemma. Two sections were previously recognized in *Piptochaetium*: *Podopogon* and *Piptochaetium*. The cladistic analysis showed that only South American species of *Piptochaetium* sect. *Piptochaetium*, together with *P. brevicalyx*, form a monophyletic group (Obovoid group), while *Piptochaetium* sect. *Podopogon* is polyphyletic. Therefore, the taxonomic recognition of sectional taxa cannot be supported. Phylogenetic relationships of two varieties of *Piptochaetium stipoides* (var. *stipoides* and var. *echinulatum*) were not clearly resolved. Furthermore, based on cladistic analyses, taxonomic observations, and the study of type material, *Piptochaetium tovarii* subsp. *pilosa* is raised to specific rank (= *P. pilosum*).

Key words: phylogenetic relationships, *Piptochaetium*, Poaceae, Stipeae.

RESUMEN

Se presenta un tratamiento sistemático de todo el género *Piptochaetium*, que complementa el propuesto por Cialdella y Arriaga para las especies sudamericanas. En este trabajo, se presenta una sinopsis de las 36 especies y 2 variedades, una clave para identificar las especies, su sinonimia, distribución geográfica y observaciones. Se incluyen por primera vez ilustraciones y fotografías de los caracteres diagnósticos para las especies norteamericanas. Se propone una hipótesis

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filogenética basada en caracteres morfológicos y anatómicos. Mediante el análisis filogenético, fue confirmada la monofilia de *Piptochaetium* sobre la base de tres sinapomorfías: una pálea surcada entre los nervios, los márgenes de la lemma involutos insertos en el surco longitudinal de la pálea y la pálea asomando por entre los márgenes de la lemma. Dos secciones fueron previamente reconocidas para *Piptochaetium*: *Podopogon* y *Piptochaetium*. Como resultado del análisis cladístico, sólo las especies sudamericanas de la sección *Piptochaetium*, junto con *P. brevicalyx*, conformaron un grupo monofilético (grupo Obovoide). Consecuentemente, en este tratamiento, no se considera válido el reconocimiento de categorías formales infragenéricas. En el análisis, se incluyeron 2 variedades de *Piptochaetium stipoides* (var. *stipoides* y var. *echinulatum*) y la posición filogenética de ambas variedades no fue claramente resuelta. *Piptochaetium tovarii* subsp. *pilosa* fue elevada al rango de especie (= *P. pilosum*), sobre la base del estudio filogenético, las observaciones taxonómicas y el estudio del material tipo.

Piptochaetium J. Presl is an American genus distributed mainly in temperate areas of both hemispheres and scarcely represented in tropical regions of the Andes (Parodi, 1944; Barkworth, 1986; Sánchez Vega, 1991; Cialdella & Arriaga, 1998). The genus belongs to the tribe Stipeae and was established by Presl in 1830, based on *Piptochaetium setifolium* J. Presl [= *P. panicoides* (Lam.) E. Desv.]. It includes perennial, caespitose plants, generally less than 1.5 m tall, with loosely or densely flowered panicles of one-flowered spikelets; membranous glumes, frequently longer than the floret, enclose the anthecium. Three characters are useful for recognizing the genus: the grooved palea, involute lemma margins that fit into a longitudinal palea groove, and the palea protruding from the lemma.

The South American species of *Piptochaetium* have been studied by Parodi (1944), who treated 21 species in 2 sections: *Piptochaetium* sect. *Podopogon* (Raf.) Parodi and *Piptochaetium* sect. *Piptochaetium* (= *Piptochaetium* sect. *Eupiptochaetium* Parodi). Sánchez Vega (1991) treated the 6 species for Peru, and grouped them into the sections proposed by Parodi. Cialdella and Arriaga (1998) published a more recent treatment of the South American species, in which they recognized 27 species, 2 subspecies, and 2 varieties for both sections, considering leaf anatomy and micromorphological characters of the lemma in their analysis. The North American taxa were studied by Valencia and Costas (1968) with emphasis on cytological characters, and they recognized 7 species. A comparison of these treatments, including the infrageneric classification, is shown in Table 1. In a revision of the North American Stipeae, Barkworth (1986) treated 13 species in North and Mesoamericas without grouping them into sections.

The aim of this work is to complete the morphological account of the genus by considering the species not included in the previous paper by Cialdella and Arriaga (1998). This study comprises a synopsis of 36 species and 2 varieties, a key to identify them, and their associated synonymy and geographical distribution. A phylogenetic analysis of *Piptochaetium* was performed to explore the relationship among species, using cladistic methodologies with the morphological data.

MATERIALS AND METHODS

MORPHOLOGICAL STUDY

This study was based on the analysis of almost 1000 herbarium specimens, including type material for most of the analyzed taxa (Appendixes 1, 2). The specimens studied were from BA, BAA, BAB, BAL, C, CAS, CEN, CORD, CPUN, CTES, G, ICN, K, LE, LP, LPB, MO, MEXU, MVM, MVFA, NY, P, PR, SGO, SI, SRFA, UNR, US, USM, UTC and XAL (Holmgren et al., 1990).

Micromorphological structures of the lemma were analyzed using a scanning microscope Zeiss DSM 940 A, located in the Instituto de Botánica Darwinion and as summarized in Cialdella and Arriaga (1998: 108). Epidermal appendages (macrohairs, prickles, hooks, and papillae) follow the classification proposed by Ellis (1979).

CLADISTIC ANALYSIS

Twenty-nine exomorphological and epidermal characters were used in the cladistic analysis (Appendix 3); all multistate characters were treated as unordered. Only two autapomorphies were included in the analyses: characters 20 and 27 (Cialdella & Arriaga, 1998: figs. 3D and 9F, respectively). Characters were directly observed from herbarium material totaling nearly 1000 specimens. The data matrix is presented in Table 2.

Two different computational strategies, using minimum parsimony, were used to analyze phylogenetic relationships among species of *Piptochaetium*. In both cases, polymorphic characters were included (Table 2). One strategy assigned all characters equal weight. This analysis was performed using NONA version 1.6 (Goloboff, 1993a). In the second strategy, a concavity function of the homoplasy (K = 3) was

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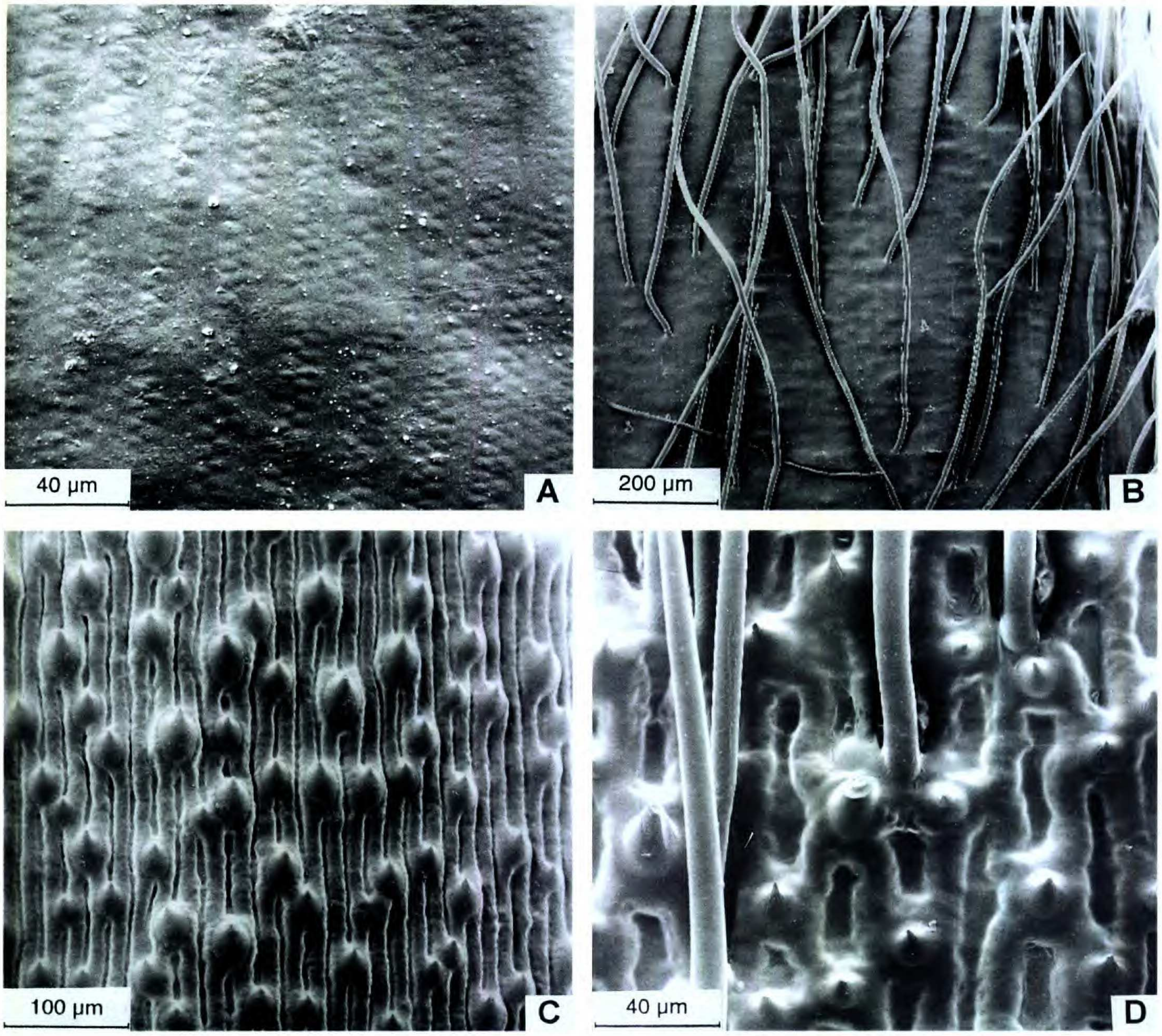

Figure 1. SEM photos showing epidermal characters of the lemma of *Piptochaetium*.—A. Lemma without any epidermal appendages of *P. brevicalyx* (*Rzedowski 35863*). —B. Macrohairs of *P. fimbriatum* (*Davidse et al. 29775*). —C. Prickles and hooks of *P. avenaceum* (*Harvey 1854*). —D. Prickles, hooks, and macrohairs of *P. angustifolium* (*Palmer 726*).

used to apply weight to all characters, a method for estimating implied weight (Goloboff, 1993b). This analysis required Pee-Wee version 2.8 (Goloboff, 1997). In both analyses, settings amb- (clades resolved only if they have unambiguous support), and poly = (polytomies allowed) were used to resolve phylogenies. The order of taxa was randomized, creating a Wagner tree and submitting it to branch-swapping by means of tree-bisection reconnection (TBR) using the sswap* command. To evaluate the relative support of clades, branch support, with instruction "bsupport" (bs) of NONA (Bremer, 1988, 1994), was calculated.

INGROUP

Since Desvaux (1853), *Piptochaetium* has been recognized by the presence of a grooved palea, and this character was diagnostic to distinguish the genus from its allies (Spegazzini, as *Oryzopsis* Michx. sensu Speg., 1901; Parodi, 1944; Barkworth, 1990; Peñailillo, 1996; Cialdella & Arriaga, 1998). Other characters were also used to uniquely identify *Piptochaetium*, such as a palea longer than the lemma, protruding from the lemma apex, and the lemma margins involute and fitted into the palea groove. The 37 entities recognized within the whole genus were considered as terminal taxa.

OUTGROUPS

Nassella E. Desv. and *Hesperostipa* (Elias) Barkworth were selected as outgroups, based on their similarities in morphological and anatomical characters to *Piptochaetium* (Thomasson, 1978b; Barkworth, 1990) as well as previous phylogenetic relationships proposed by Barkworth (1990).

A detailed history of *Nassella* can be found in

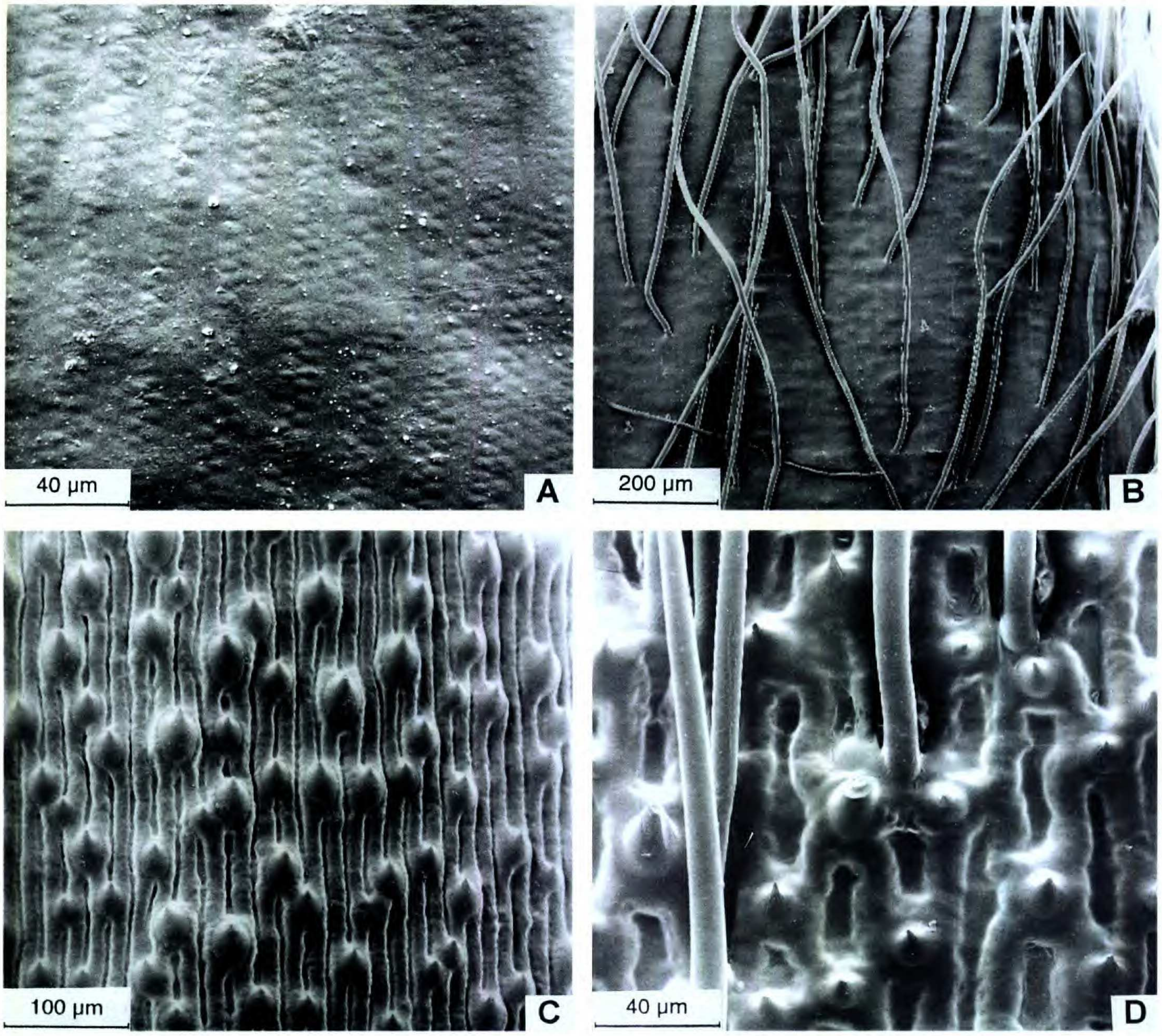

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Table 1. Infrageneric classifications within *Piptochaetium* in comparison with results from the phylogenetic analysis. Geographic distribution of the species is also presented. Abbreviations correspond to: Ar, Argentina; Bo, Bolivia; Br, Brazil; Ch, Chile; Co, Colombia; Ec, Ecuador; Gu, Guatemala, Me, Mexico; Pa, Paraguay; Pe, Peru; Ur, Uruguay; US, United States; Ve, Venezuela.

Sections sensu Parodi (1944)	Valencia & Costas (1968)	Sanchez Vega (1991)	Cialdella & Arriaga (1998)	Informal groups from the phylogenetic analysis	Geographical distribution
PODOPOGON	PODOPOGON	PODOPOGON	PODOPOGON	Polyphyletic group	
			P. alpinum	*P. alpinum*	Br
P. angustifolium ?				*P. angustifolium*	Me
P. avenaceum	*P. avenaceum*			*P. avenaceum*	Me, US
P. avenacioides ?	*P. avenacioides*			*P. avenacioides*	US
P. bicolor			*P. bicolor*	*P. bicolor*	Ar, Ch, Ur
P. brachyspermum			*P. brachyspermum*	*P. brachyspermum*	Ar
P. cabrerae			*P. cabrerae*	*P. cabrerae*	Ar
P. confusum			*P. confusum*	*P. confusum*	Ar, Ur
		P. featherstonei	*P. featherstonei*	*P. featherstonei*	Pe
				P. fimbriatum	Gu, Me, US
P. hackelii			*P. hackelii*	*P. hackelii*	Ar, Ur
P. indutum		*P. indutum*	*P. indutum*	*P. indutum*	Ar, Bo, Ec, Pe
= *P. bicolor*			*P. medium*	*P. medium*	Ar, Br, Ur
P. napostaense			*P. napostaense*	*P. napostaense*	Ar
			P. palustre	*P. palustre*	Br
				P. pringlei	Me, US
P. ruprechtianum			*P. ruprechtianum*	*P. ruprechtianum*	Ar, Br, Ur
		P. sagasteguii	*P. sagasteguii*	*P. sagasteguii*	Pe
				P. seleri	Gu, Me
P. virescens	*P. virescens*			*P. virescens*	Gu, Me, Ve
PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	Obovoid Group	
	P. angustifolium				Me
P. angolense			*P. angolense*	*P. angolense*	Ch
P. brevicalyx	*P. brevicalyx*			*P. brevicalyx*	Me
P. burkartianum			*P. burkartianum*	*P. burkartianum*	Ar
P. calvescens			*P. calvescens*	*P. calvescens*	Ar, Ur
			P. cucullatum	*P. cucullatum*	Ur
P. fimbriatum	*P. fimbriatum*				Gu, Me, US
P. hirtum			*P. hirtum*	*P. hirtum*	Ar, Ch
P. jubatum			*P. jubatum*	*P. jubatum*	Ur

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			P. alpinum	*P. alpinum*	Br
P. angustifolium ?				*P. angustifolium*	Me
P. avenaceum	*P. avenaceum*			*P. avenaceum*	Me, US
P. avenacioides ?	*P. avenacioides*			*P. avenacioides*	US
P. bicolor			*P. bicolor*	*P. bicolor*	Ar, Ch, Ur
P. brachyspermum			*P. brachyspermum*	*P. brachyspermum*	Ar
P. cabrerae			*P. cabrerae*	*P. cabrerae*	Ar
P. confusum			*P. confusum*	*P. confusum*	Ar, Ur
		P. featherstonei	*P. featherstonei*	*P. featherstonei*	Pe
				P. fimbriatum	Gu, Me, US
P. hackelii			*P. hackelii*	*P. hackelii*	Ar, Ur
P. indutum		*P. indutum*	*P. indutum*	*P. indutum*	Ar, Bo, Ec, Pe
= *P. bicolor*			*P. medium*	*P. medium*	Ar, Br, Ur
P. napostaense			*P. napostaense*	*P. napostaense*	Ar
			P. palustre	*P. palustre*	Br
				P. pringlei	Me, US
P. ruprechtianum			*P. ruprechtianum*	*P. ruprechtianum*	Ar, Br, Ur
		P. sagasteguii	*P. sagasteguii*	*P. sagasteguii*	Pe
				P. seleri	Gu, Me
P. virescens	*P. virescens*			*P. virescens*	Gu, Me, Ve
PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	Obovoid Group	
	P. angustifolium				Me
P. angolense			*P. angolense*	*P. angolense*	Ch
P. brevicalyx	*P. brevicalyx*			*P. brevicalyx*	Me
P. burkartianum			*P. burkartianum*	*P. burkartianum*	Ar
P. calvescens			*P. calvescens*	*P. calvescens*	Ar, Ur
			P. cucullatum	*P. cucullatum*	Ur
P. fimbriatum	*P. fimbriatum*				Gu, Me, US
P. hirtum			*P. hirtum*	*P. hirtum*	Ar, Ch
P. jubatum			*P. jubatum*	*P. jubatum*	Ur

Table 1. Continued.

Sections sensu Parodi (1944)	Valencia & Costas (1968)	Sanchez Vega (1991)	Cialdella & Arriaga (1998)	Informal groups from the phylogenetic analysis	Geographical distribution
P. lasianthum			*P. lasianthum*	*P. lasianthum*	Ar, Br, Ur
P. lejopodum			*P. lejopodum*	*P. lejopodum*	Ar, Ur
P. montevidense		*P. montevidense*	*P. montevidense*	*P. montevidense*	Ar, Bo, Br, Ch, Ec, Me, Pa, Pe, Ve, Ur
P. panicoides		*P. panicoides*	*P. panicoides*	*P. panicoides*	Ar, Bo, Br, Ch, Co, Ec, Pe, Ve, Ur
		= *P. tovari* subsp. *pilosa*	= *P. tovari* subsp. *pilosa*	*P. pilosum*	Pe
P. pringlei	*P. pringlei*				Me, US
P. setosum			*P. setosum*	*P. setosum*	Ch, US
P. stipoides var. *echinulatum*			*P. stipoides* var. *echinulatum*	*P. stipoides* var. *echinulatum*	Ar, Ur
P. stipoides var. *stipoides*			*P. stipoides* var. *stipoides*	*P. stipoides* var. *stipoides*	Ar, Br, Ch, Me, US, Ur
		= *P. tovari* subsp. *tovarii*	= *P. tovari* subsp. *tovarii*	*P. tovarii*	Ec, Pe
P. uruguense			*P. uruguense*	*P. uruguense*	Ar, Br, Me, Pa, Ur

Barkworth (1990). She expanded *Nassella*, including a total of 79 species, the majority of which were previously considered in *Stipa* L. The circumscription proposed by Barkworth (1990) was later accepted by Peñailillo (1996) and Torres (1997). In this sense, *Nassella* includes species with obovoid or terete florets, a short and blunt to long and sharp callus, strongly overlapping lemma margins, a lemma apex fused in a crown, and a highly reduced, nerveless and glabrous palea. All species considered in *Nassella* have a characteristic lemma epidermal pattern: short fundamental cells, with irregularly sinuate sidewalls and abundant short cells.

Hesperostipa was one of the nine sections of *Stipa* formally proposed by Elias (1942). Thomasson (1978a) noticed a very different epidermal pattern within this section in comparison with any other *Stipa*: long fundamental cells with strongly sinuous sidewalls, and absence of short cells. After studying North American Stipeae, Barkworth (1993) raised *Stipa* sect. *Hesperostipa* to the generic rank, in which she included four species: *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *H. curtiseta* (Hitchc.) Barkworth, *H. neomexicana* (Thurber) Barkworth, and *H. spartea* (Trin.) Barkworth. *Hesperostipa* is endemic to North America and includes plants with narrowly terete florets, a sharp callus, and a persistent, twice-geniculate awn. The lemma is indurate, with flat margins, slightly or not overlapping; the palea is subequal to the lemma, prow tipped and 2-nerved (Barkworth, 1993).

KEY TO *PIPTOCHAETIUM*, *NASSELLA*, AND *HESPEROSTIPA*

1. Palea longitudinally grooved, 2-nerved, longer than the lemma, and protruding from the lemma apex; lemma margins involute, fitting into the palea groove .... *Piptochaetium*

1′. Palea flat, 2-nerved or nerveless, shorter than or equal to the lemma, usually not protruding beyond the lemma apex; lemma margins flat 2

2(1). Lemma margins strongly overlapping; palea nerveless, less than one-third the length of the lemma .... *Nassella*

2′. Lemma margins not or slightly overlapping; palea 2-nerved, always as long as the lemma, apex prow tipped or "pinched" .... *Hesperostipa*

RESULTS

Seven equally parsimonious trees were obtained when the characters were weighted equally. These were 58 steps long, with a Consistency Index (CI) = 0.55 and Retention Index (RI) = 0.87. When the analysis was performed without autapomorphies (characters 20 and 27), the CI was 0.53. When the characters were weighted, five equally parsimonious

Table 1. Continued.

Sections sensu Parodi (1944)	Valencia & Costas (1968)	Sanchez Vega (1991)	Cialdella & Arriaga (1998)	Informal groups from the phylogenetic analysis	Geographical distribution
P. lasianthum			*P. lasianthum*	*P. lasianthum*	Ar, Br, Ur
P. lejopodum			*P. lejopodum*	*P. lejopodum*	Ar, Ur
P. montevidense		*P. montevidense*	*P. montevidense*	*P. montevidense*	Ar, Bo, Br, Ch, Ec, Me, Pa, Pe, Ve, Ur
P. panicoides		*P. panicoides*	*P. panicoides*	*P. panicoides*	Ar, Bo, Br, Ch, Co, Ec, Pe, Ve, Ur
		= *P. tovari* subsp. *pilosa*	= *P. tovari* subsp. *pilosa*	*P. pilosum*	Pe
P. pringlei	*P. pringlei*				Me, US
P. setosum			*P. setosum*	*P. setosum*	Ch, US
P. stipoides var. *echinulatum*			*P. stipoides* var. *echinulatum*	*P. stipoides* var. *echinulatum*	Ar, Ur
P. stipoides var. *stipoides*			*P. stipoides* var. *stipoides*	*P. stipoides* var. *stipoides*	Ar, Br, Ch, Me, US, Ur
		= *P. tovari* subsp. *tovarii*	= *P. tovari* subsp. *tovarii*	*P. tovarii*	Ec, Pe
P. uruguense			*P. uruguense*	*P. uruguense*	Ar, Br, Me, Pa, Ur

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Table 2. Data matrix used in the cladistic analyses for *Piptochaetium.* Numbers in the first row represent the characters described in the text, together with their codification. Numbers within brackets represent a polymorphism for the particular character of the species involved.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Nassella	0	0	2	0	0	0	[0 1]	[0 1]	[0 1]	[0 1]	[0 1]	0	[0 2 3]	[0 1]	[0 1]
Hesperostipa	0	0	0	1	1	2	1	0	1	0	[0 1]	0	0	0	[0 1]
Piptochaetium alpinum	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1
P. angolense	1	1	1	1	1	1	0	1	1	1	0	0	2	1	0
P. angustifolium	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
P. avenaceum	1	1	1	1	1	1	1	0	1	0	[0 1]	0	0	0	0
P. avenacioides	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. bicolor	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brachyspermum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brevicalyx	1	1	1	1	1	1	0	1	0	1	0	1	2	0	0
P. burkartianum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. cabrerae	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
P. calvescens	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. confusum	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. cucullatum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. featherstonei	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. fimbriatum	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. hackelii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. hirtum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. indutum	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. jubatum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. lasianthum	1	1	1	1	1	1	0	1	1	1	1	0	2	0	1
P. lejopodum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. medium	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. montevidense	1	1	1	1	1	1	0	1	0	1	[0 1]	0	3	1	0
P. napostaense	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. palustre	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. panicoides	1	1	1	1	1	1	0	1	0	1	0	0	3	1	0
P. pilosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	1
P. pringlei	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. ruprechtianum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. sagasteguii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. seleri	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. setosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	0
P. stipoides var. *echinulatum*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. stipoides var. *stipoides*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. tovarii	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. uruguense	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. virescens	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1

trees were obtained. These trees were also 58 steps long, their fit was 190.7, and the rescaled fit was 0.68. Although the trees obtained with the two strategies differed in some respects, both yielded the same strict consensus tree as well as the unambiguous synapomorphies that support clades (Fig. 3). Only the relationships within one clade, which involved *P. calvescens, P. cucullatum, P. jubatum, P. lejopodum, P. stipoides* var. *stipoides*, and *P. stipoides* var. *echinulatum*, differed between the strategies. Relationships among these species are not resolved on the consensus tree (Fig. 3). Figure 4 shows one of the seven hypotheses found with NONA. This tree is the most similar to one of the five trees found with Pee-Wee. They differ in the position of *P. alpinum* which, in Pee-Wee's results, is sister to the clade that includes *P. pringlei* to *P. palustre*; and they also differ in the order of *P. uruguense* and *P. angolense*, which are inverted in Pee-Wee analysis.

Cladistic analysis supports *Piptochaetium* as a monophyletic genus [Bremer support (bs) = 3]. It is clearly defined by three synapomorphies (Fig. 3): lemma margins involute (1), a boat-shaped palea (2), and a palea longer than the lemma (3; Fig. 2A, B).

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	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Nassella	0	0	2	0	0	0	[0 1]	[0 1]	[0 1]	[0 1]	[0 1]	0	[0 2 3]	[0 1]	[0 1]
Hesperostipa	0	0	0	1	1	2	1	0	1	0	[0 1]	0	0	0	[0 1]
Piptochaetium alpinum	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1
P. angolense	1	1	1	1	1	1	0	1	1	1	0	0	2	1	0
P. angustifolium	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
P. avenaceum	1	1	1	1	1	1	1	0	1	0	[0 1]	0	0	0	0
P. avenacioides	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. bicolor	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brachyspermum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brevicalyx	1	1	1	1	1	1	0	1	0	1	0	1	2	0	0
P. burkartianum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. cabrerae	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
P. calvescens	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. confusum	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. cucullatum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. featherstonei	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. fimbriatum	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. hackelii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. hirtum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. indutum	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. jubatum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. lasianthum	1	1	1	1	1	1	0	1	1	1	1	0	2	0	1
P. lejopodum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. medium	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. montevidense	1	1	1	1	1	1	0	1	0	1	[0 1]	0	3	1	0
P. napostaense	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. palustre	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. panicoides	1	1	1	1	1	1	0	1	0	1	0	0	3	1	0
P. pilosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	1
P. pringlei	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. ruprechtianum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. sagasteguii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. seleri	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. setosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	0
P. stipoides var. *echinulatum*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. stipoides var. *stipoides*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. tovarii	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. uruguense	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. virescens	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1

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Table 2. Extended.

	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Nassella	[0 1]	[0 1]	[0 1]	0	0	[0 1]	[0 1]	0	[0 1]	0	[0 1]	0	[0 1]	0
Hesperostipa	0	1	1	0	0	0	1	0	1	0	1	0	0	0
Piptochaetium alpinum	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. angolense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. angustifolium	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. avenaceum	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. avenacioides	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. bicolor	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. brachyspermum	0	1	0	1	0	1	1	1	0	0	1	0	0	0
P. brevicalyx	0	0	0	0	0	1	1	0	0	0	0	0	1	0
P. burkartianum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. cabrerae	0	1	1	0	0	1	1	1	0	0	1	0	0	0
P. calvescens	[0 1]	1	1	0	0	1	0	1	0	1	1	0	1	1
P. confusum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. cucullatum	0	1	0	1	0	1	1	1	0	0	1	1	1	0
P. featherstonei	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. fimbriatum	0	0	0	0	0	1	1	0	[0 1]	0	[0 1]	0	1	0
P. hackelii	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. hirtum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. indutum	0	1	1	0	0	0	1	0	0	0	1	0	0	0
P. jubatum	0	1	0	1	0	1	[0 1]	1	1	0	1	0	1	1
P. lasianthum	0	1	1	0	0	1	1	0	1	0	1	0	1	0
P. lejopodum	0	1	0	1	0	1	0	1	0	0	1	0	1	1
P. medium	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. montevidense	1	0	0	0	0	1	1	0	0	1	1	0	1	0
P. napostaense	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. palustre	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. panicoides	[0 1]	0	0	0	0	1	1	0	0	1	1	0	1	0
P. pilosum	0	1	1	0	0	0	1	0	0	0	1	0	1	0
P. pringlei	0	0	0	0	0	1	1	0	1	0	1	0	0	0
P. ruprechtianum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. sagasteguii	0	1	1	0	0	0	1	0	1	0	1	0	0	0
P. seleri	0	1	1	0	0	1	1	0	1	0	1	0	[0 1]	0
P. setosum	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. stipoides var. *echinulatum*	0	1	1	0	1	1	0	1	0	1	1	0	1	1
P. stipoides var. *stipoides*	0	[0 1]	[0 1]	[0 1]	0	1	[0 1]	1	[0 1]	[0 1]	[0 1]	0	1	[0 1]
P. tovarii	0	0	0	0	0	0	1	0	0	0	0	0	1	0
P. uruguense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. virescens	0	1	1	0	0	0	1	0	1	0	1	0	0	0

Hesperostipa is the most closely related group to *Piptochaetium*, as they share a 2-nerved palea (4) and long fundamental cells of the lemma epidermis (5).

South American species of *Piptochaetium* sect. *Piptochaetium*, together with *P. brevicalyx* from Mexico, are gathered in a monophyletic clade (bs = 2), which is now recognized herein as the Obovoid group (Fig. 3). It is supported by two synapomorphies: a deciduous awn (10) and obovoid florets (13, Fig. 5H). Three species are closely related to the Obovoid clade: *P. fimbriatum* (Fig. 5G), *P. seleri* (Fig. 5F), and *P. angustifolium* (Fig. 5E). *Piptochaetium fimbriatum* and *P. seleri* present a blunt or truncate callus (8; bs = 1) and, together with *P. angustifolium*, they all have a short callus (7; bs = 1). These three species are not included in the Obovoid clade, as they do not have a deciduous awn as well as a well-defined obovoid floret. They are North American species; *P. fimbriatum* and *P. seleri* were also found in Guatemala, with intermediate forms observed between the Obovoid clade and the rest of the species (Figs. 3 and 4; see discussion). Species of the Obovoid clade present the relation between length and width of the floret always less than 3.5

Table 2. Extended.

	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Nassella	[0 1]	[0 1]	[0 1]	0	0	[0 1]	[0 1]	0	[0 1]	0	[0 1]	0	[0 1]	0
Hesperostipa	0	1	1	0	0	0	1	0	1	0	1	0	0	0
Piptochaetium alpinum	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. angolense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. angustifolium	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. avenaceum	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. avenacioides	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. bicolor	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. brachyspermum	0	1	0	1	0	1	1	1	0	0	1	0	0	0
P. brevicalyx	0	0	0	0	0	1	1	0	0	0	0	0	1	0
P. burkartianum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. cabrerae	0	1	1	0	0	1	1	1	0	0	1	0	0	0
P. calvescens	[0 1]	1	1	0	0	1	0	1	0	1	1	0	1	1
P. confusum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. cucullatum	0	1	0	1	0	1	1	1	0	0	1	1	1	0
P. featherstonei	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. fimbriatum	0	0	0	0	0	1	1	0	[0 1]	0	[0 1]	0	1	0
P. hackelii	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. hirtum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. indutum	0	1	1	0	0	0	1	0	0	0	1	0	0	0
P. jubatum	0	1	0	1	0	1	[0 1]	1	1	0	1	0	1	1
P. lasianthum	0	1	1	0	0	1	1	0	1	0	1	0	1	0
P. lejopodum	0	1	0	1	0	1	0	1	0	0	1	0	1	1
P. medium	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. montevidense	1	0	0	0	0	1	1	0	0	1	1	0	1	0
P. napostaense	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. palustre	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. panicoides	[0 1]	0	0	0	0	1	1	0	0	1	1	0	1	0
P. pilosum	0	1	1	0	0	0	1	0	0	0	1	0	1	0
P. pringlei	0	0	0	0	0	1	1	0	1	0	1	0	0	0
P. ruprechtianum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. sagasteguii	0	1	1	0	0	0	1	0	1	0	1	0	0	0
P. seleri	0	1	1	0	0	1	1	0	1	0	1	0	[0 1]	0
P. setosum	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. stipoides var. *echinulatum*	0	1	1	0	1	1	0	1	0	1	1	0	1	1
P. stipoides var. *stipoides*	0	[0 1]	[0 1]	[0 1]	0	1	[0 1]	1	[0 1]	[0 1]	[0 1]	0	1	[0 1]
P. tovarii	0	0	0	0	0	0	1	0	0	0	0	0	1	0
P. uruguense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. virescens	0	1	1	0	0	0	1	0	1	0	1	0	0	0

Hesperostipa is the most closely related group to *Piptochaetium*, as they share a 2-nerved palea (4) and long fundamental cells of the lemma epidermis (5).

South American species of *Piptochaetium* sect. *Piptochaetium*, together with *P. brevicalyx* from Mexico, are gathered in a monophyletic clade (bs = 2), which is now recognized herein as the Obovoid group (Fig. 3). It is supported by two synapomorphies: a deciduous awn (10) and obovoid florets (13, Fig. 5H). Three species are closely related to the Obovoid clade: *P. fimbriatum* (Fig. 5G), *P. seleri* (Fig. 5F), and *P. angustifolium* (Fig. 5E). *Piptochaetium fimbriatum* and *P. seleri* present a blunt or truncate callus (8; bs = 1) and, together with *P. angustifolium*, they all have a short callus (7; bs = 1). These three species are not included in the Obovoid clade, as they do not have a deciduous awn as well as a well-defined obovoid floret. They are North American species; *P. fimbriatum* and *P. seleri* were also found in Guatemala, with intermediate forms observed between the Obovoid clade and the rest of the species (Figs. 3 and 4; see discussion). Species of the Obovoid clade present the relation between length and width of the floret always less than 3.5

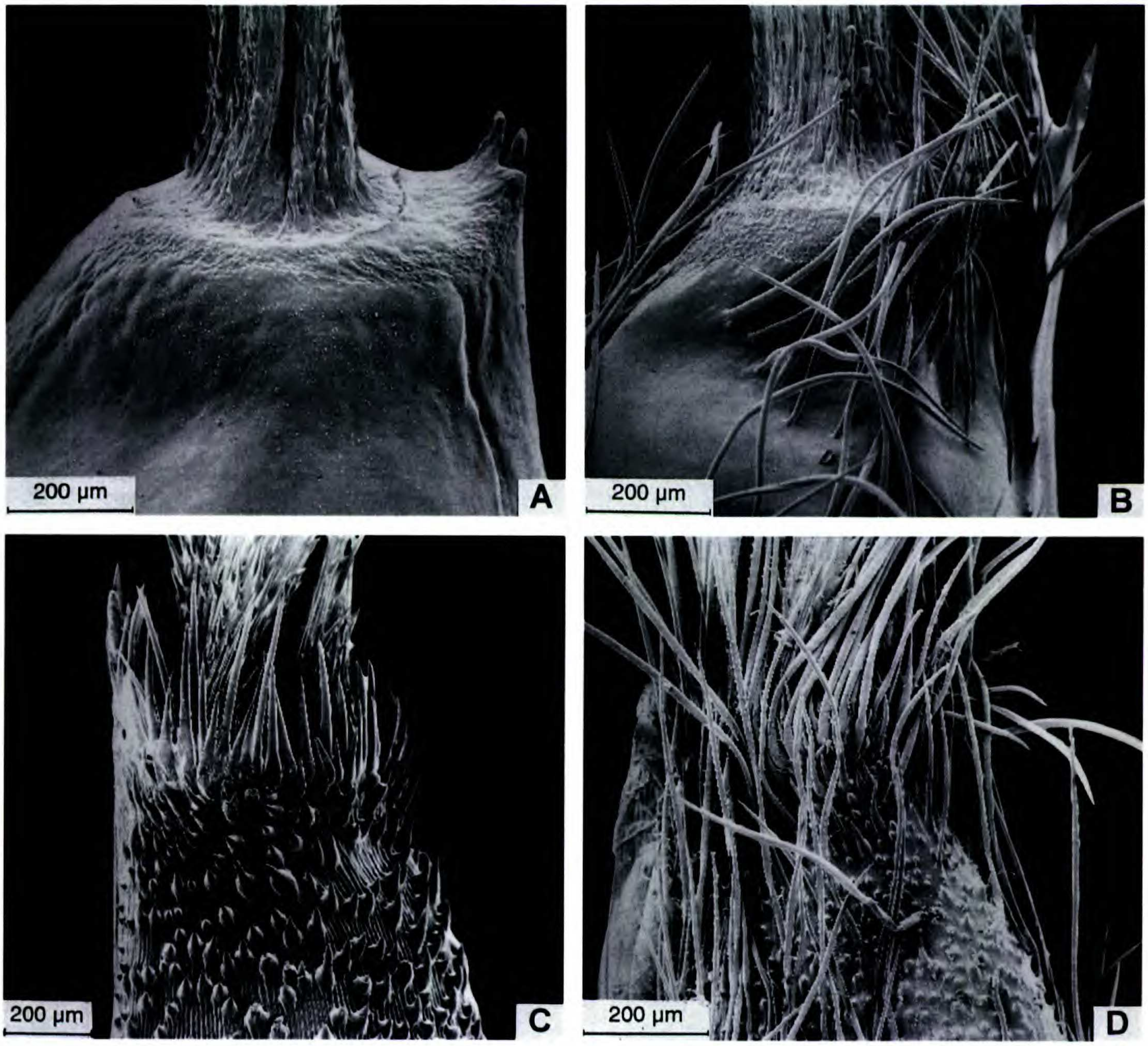
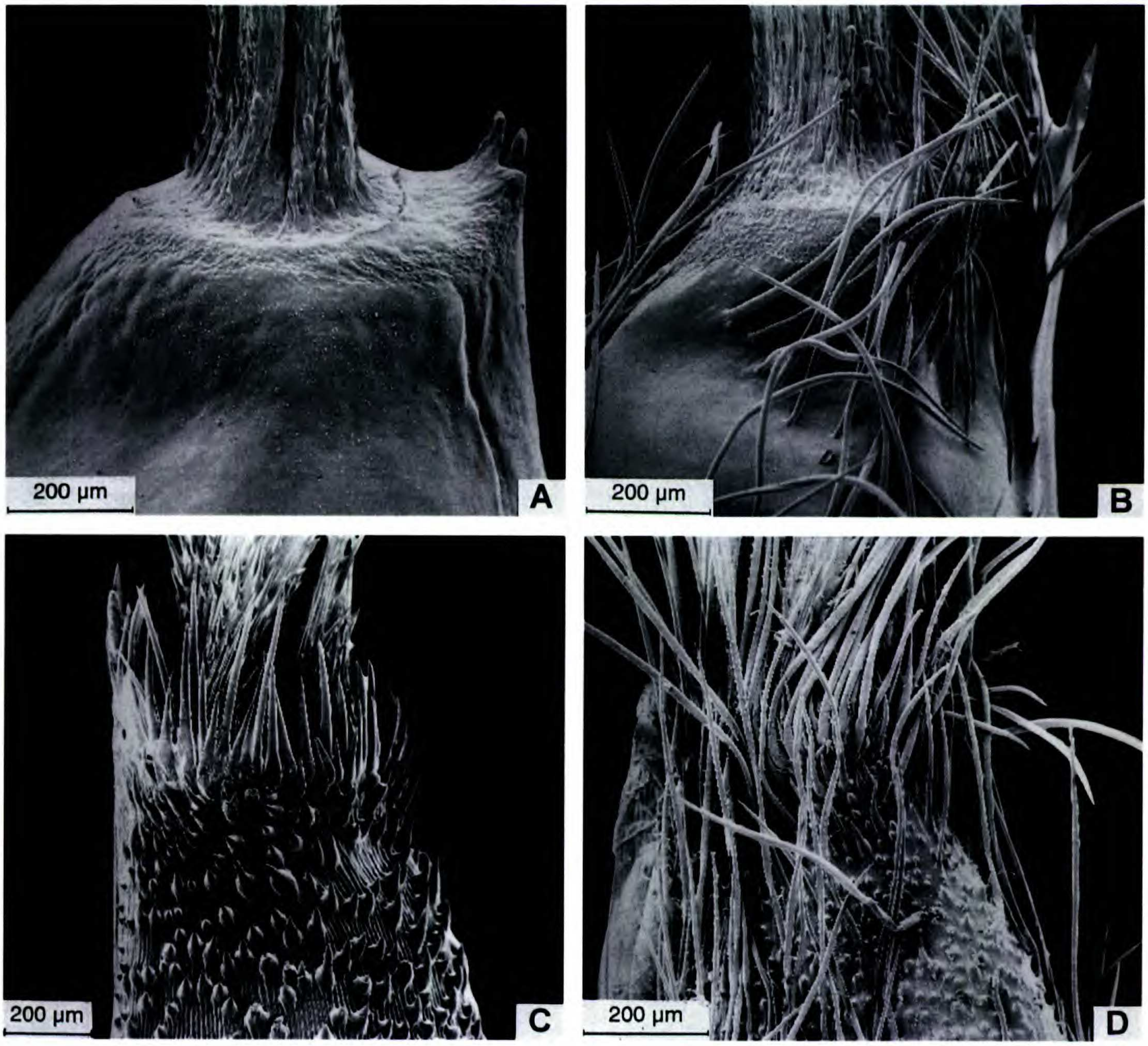


Figure 2. SEM photos showing distal portion of the floret with different crowns in *Piptochaetium*.—A. *P. brevicalyx* (*Rzedowski 35863*). —B. *P. fimbriatum* (*Davidse et al. 29775*). —C. *P. avenaceum* (*Harvey 1854*). —D. *P. angustifolium* (*Palmer 726*).

(28). However, this character is ambiguous for the clade that gathers the Obovoid group with *P. seleri* and *P. fimbriatum*, and consequently, this synapomorphy is not shown in Figure 3. An additional analysis was performed to test the influence of the intermediate species (*P. fimbriatum*, *P. angustifolium*, and *P. seleri*) on the results. Without these three species, the major clades and relationships among the species did not change.

All species of the Obovoid clade, except *P. lasianthum*, have densely flowered inflorescences (11), although for some species of this clade this character is variable. These species also have a crown without macrohairs (24), which reverts in *P. jubatum* and is polymorphic in *P. stipoides* var. *stipoides*. Species from *P. uruguense* to *P. stipoides* var. *echinulatum* form a clade defined by a glabrous lemma (15, Fig. 1A, 5H; bs = 1), and *P. pilosum* (= *P. tovarii* var. *pilosa* Sánchez Vega) is consequently apart from its counterpart *P. tovarii* (= *P. tovarii* var. *tovarii*), suggesting this rank is not appropriate. Species with a few prickles on the lemma (18) are gathered in a clade that includes species from *P. burkartianum* to *P. stipoides* var. *echinulatum* (bs = 1). This grouping is divided into two major clades. The first clade, *P. burkartianum*, *P. montevidense*, *P. panicoides*, *P. hirtum*, *P. brevicalyx*, and *P. tovarii* (bs = 1), is characterized by a lemma without prickles (17, Fig. 1A), and, except for *P. burkartianum*, the other species also have a glabrous callus (9; bs = 1). *Piptochaetium brevicalyx* and *P. tovarii* are related by the absence of prickles in the crown (26; bs = 1), while *P. montevidense* and *P. panicoides* are gathered in a clade (bs = 3) and share three synapomorphies: lens-shaped (13) and laterally compressed florets (14), and presence of papillae in the crown (25).



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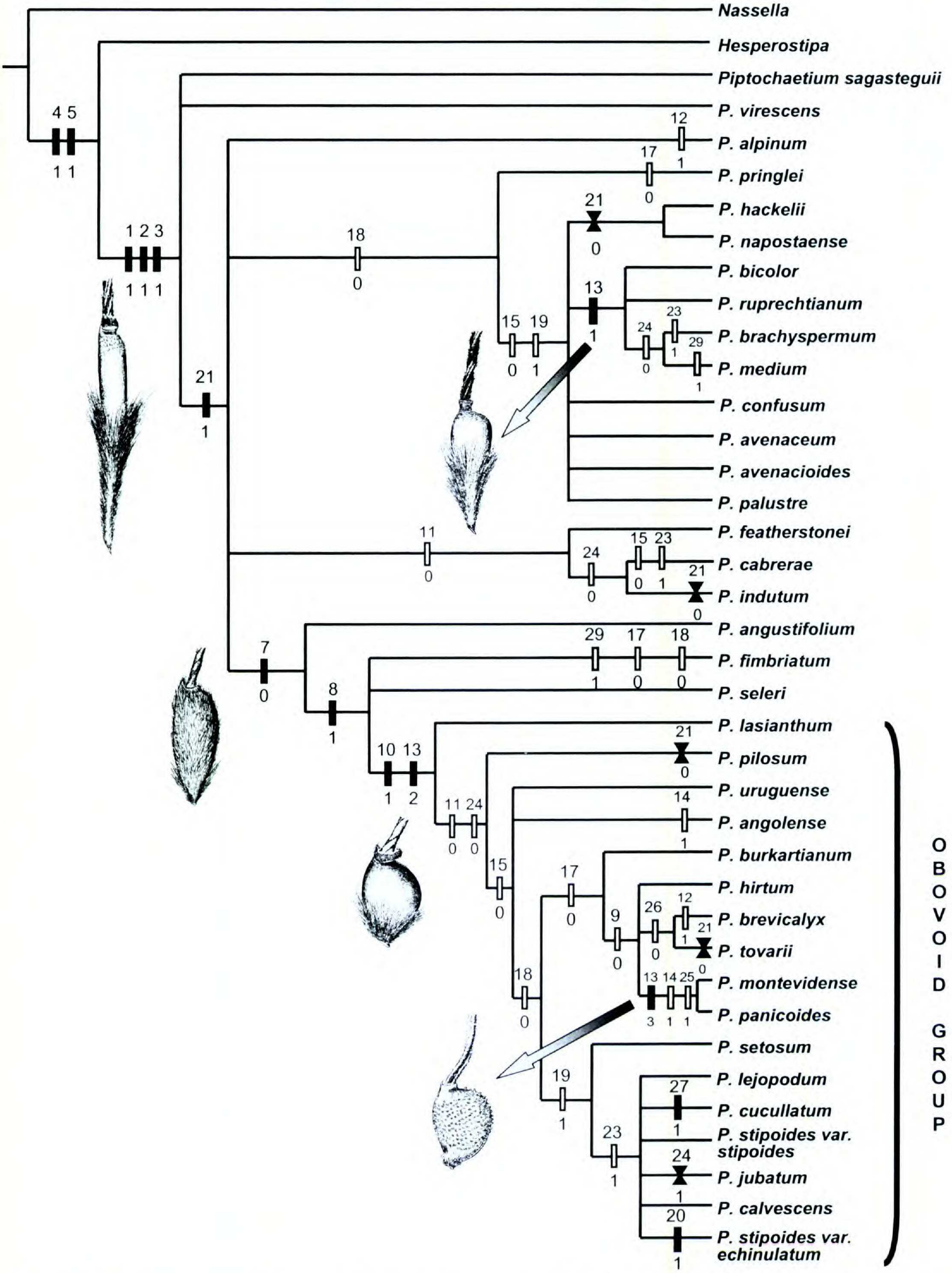
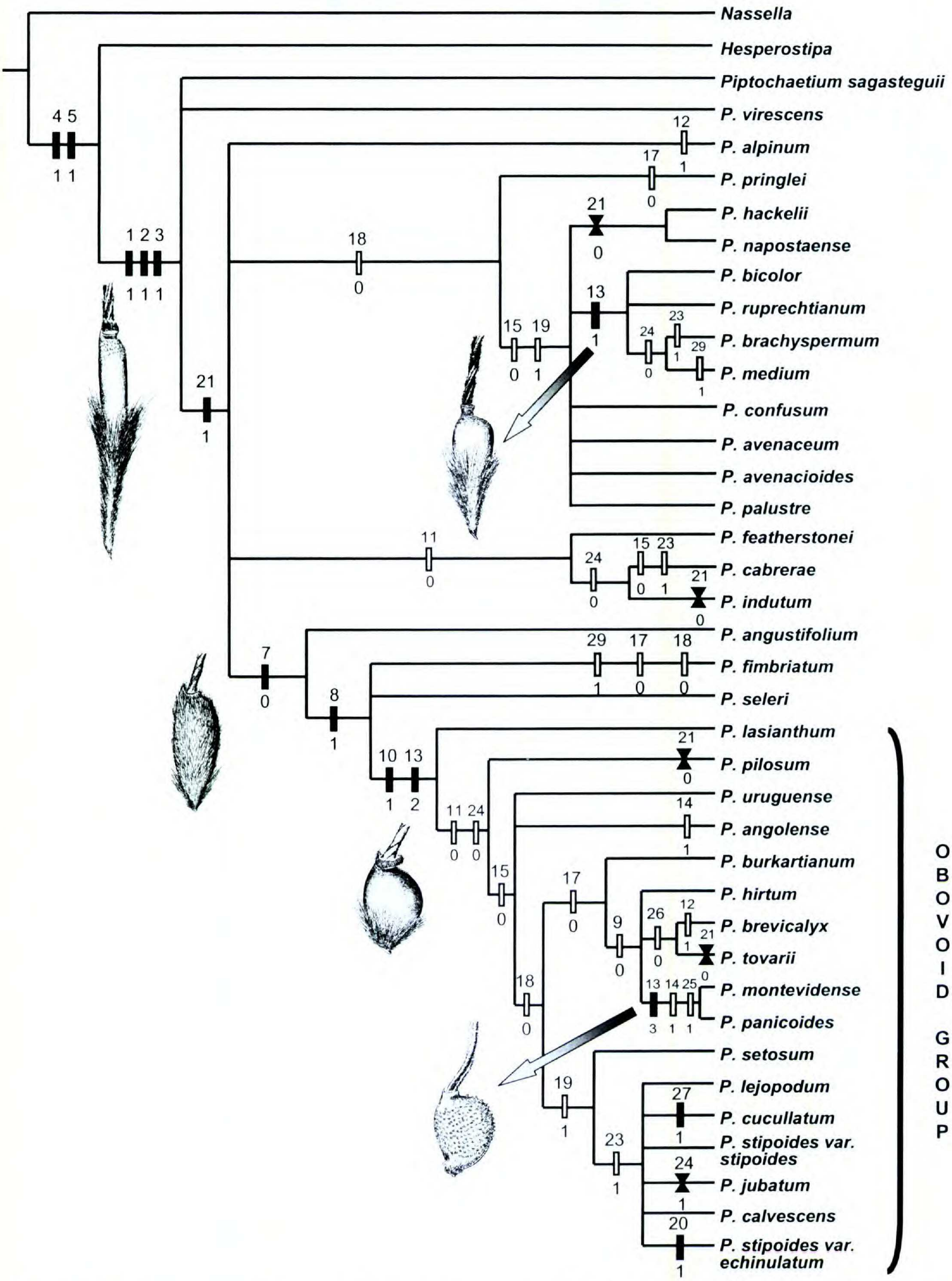


Figure 3. Strict consensus of seven equally parsimonious trees resulting from phylogenetic analysis of *Piptochaetium* (NONA program). A similar tree resulted from the strict consensus of five equally parsimonious trees under implied weight (Pee-wee program). Optimization of characters are shown on the tree: solid bars = unambiguous synapomorphies, empty bars = homoplastic character transformations, solid crosses = reversals. Character numbers (see Appendix 3) are above symbols, and character state changes are below bar or crosses. Illustrations show evolution of floret shape in *Piptochaetium* (see discussion).



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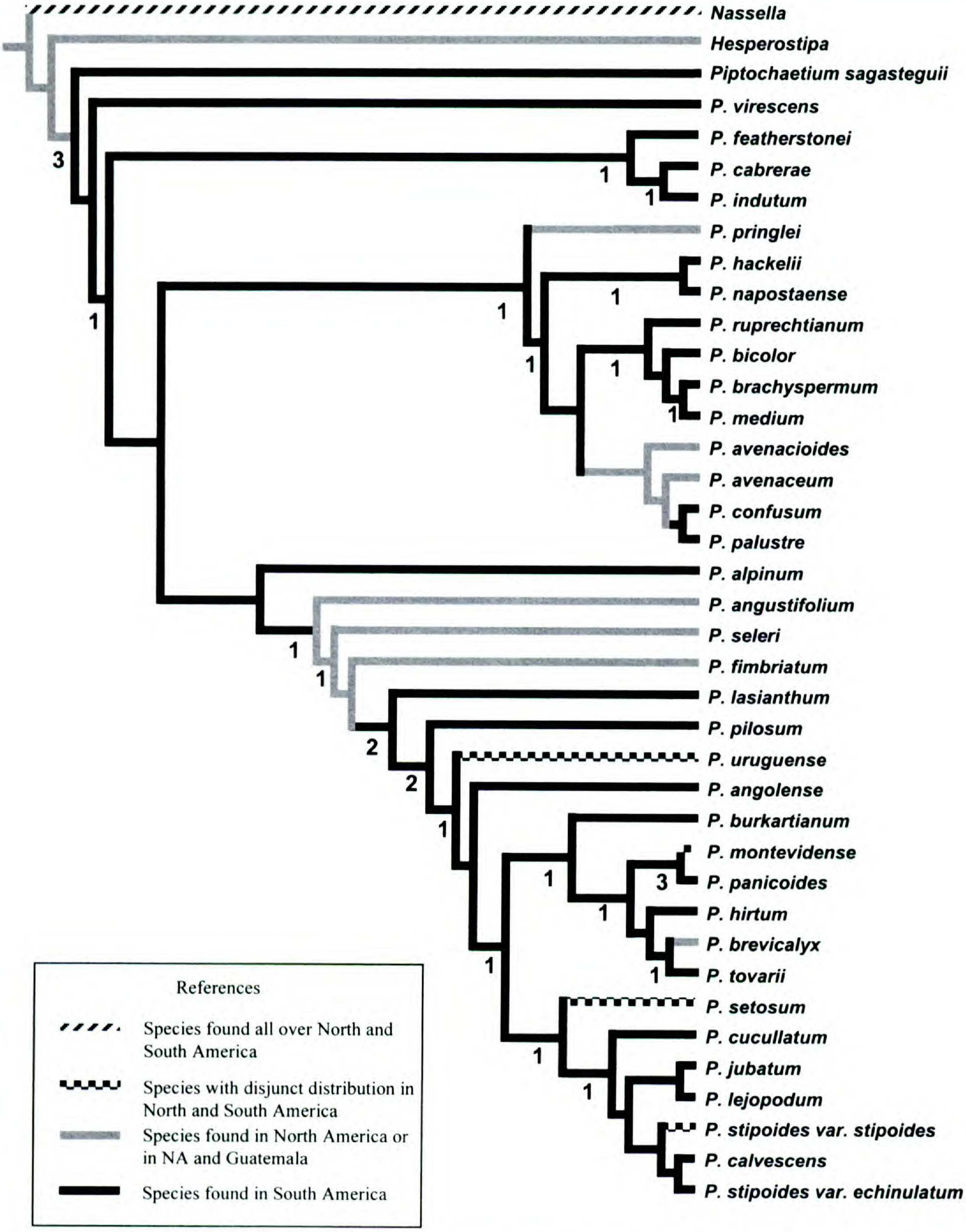
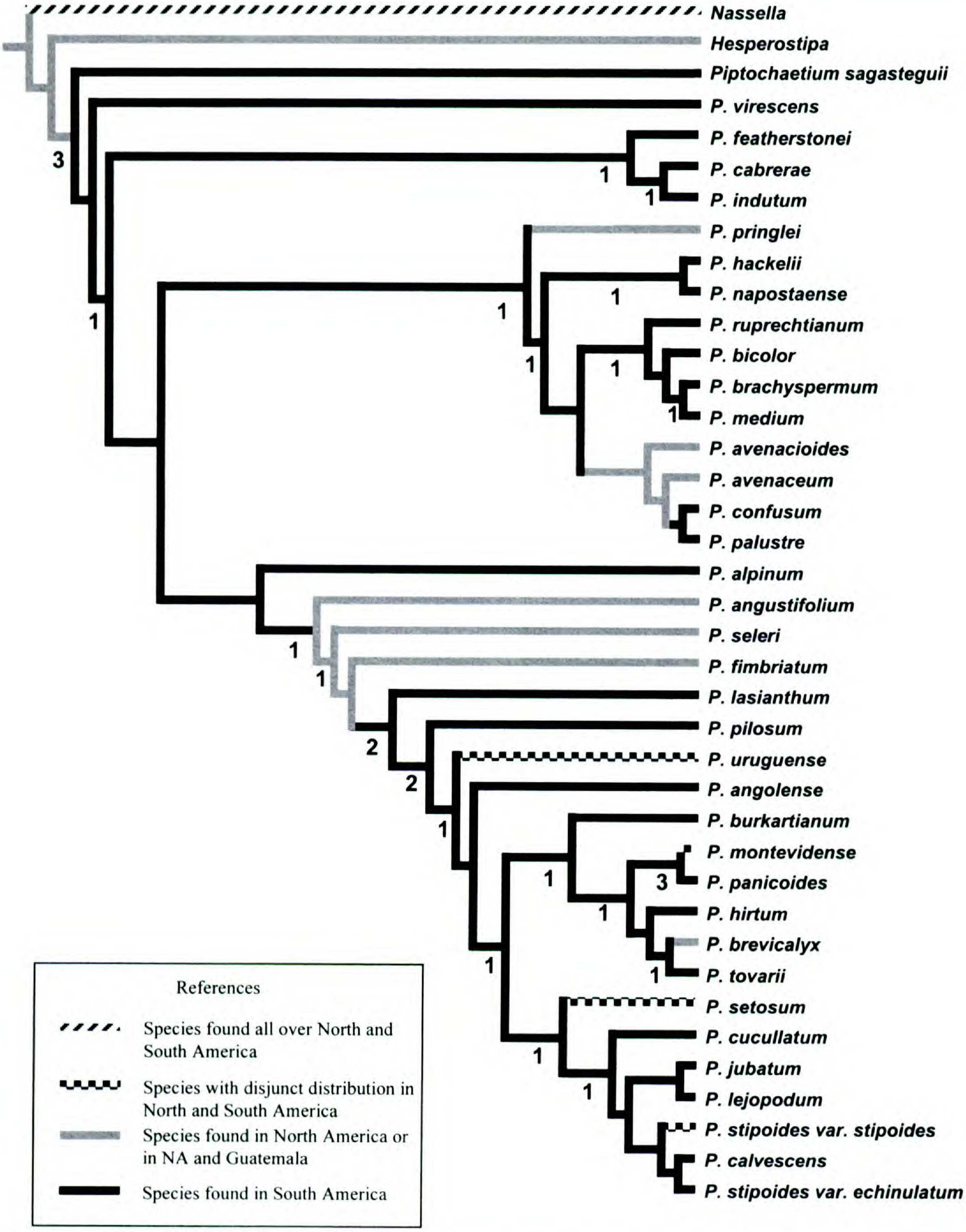


Figure 4. One of the seven equally parsimonious trees of 58 steps resulting from the phylogenetic analysis of *Piptochaetium* (NONA program), based on morphological and epidermal characters. Distribution of species is mapped on the tree as shown in the references. Numbers below branches represent the Bremer support value for each clade.

Lateral compression of the floret (14) is a derived character that occurs also in *P. angolense* (Cialdella & Arriaga, 1998: fig. 9C). The second major clade comprises *P. setosum*, *P. calvescens*, *P. cucullatum*, *P. jubatum*, *P. lejopodum*, and two varieties of *P. stipoides* (bs = 1). This clade is characterized by the presence of prickles in only one-third of the lemma (19), except *P. stipoides* var. *echinulatum*, which has prickles on almost all the lemma surface. With the exception of *P. setosum*, all other species have a rev-



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Species traditionally included in *Piptochaetium* sect. *Podopogon* (Cialdella & Arriaga, 1998) resulted in a polyphyletic group. Species of this section are linked to some North American species, not included in any previous infrageneric classification (Table 1, Fig. 3). Some species of this section are gathered in stable clades based on unambiguous synapomorphies: *P. featherstonei*, *P. cabrerae*, and *P. indutum* have loosely flowered inflorescence branches (11; bs = 1), while *P. cabrerae* and *P. indutum* do not have macrohairs in the crown (24; bs = 1). *Piptochaetium cabrerae* is characterized by a glabrous lemma (15) and a revolute crown (23). A clade including *P. pringlei* (Fig. 5D) to *P. palustre* is distinguished by the absence of prickles over almost the entire lemma surface (18; bs = 1). All species of this clade (bs = 1), except *P. pringlei*, have a glabrous lemma (15), with prickles restricted to the distal third (19). *Piptochaetium hackelii* and *P. napostaense* are identified by a lemma as wide as the crown (21; bs = 1). This character appears as reversals in *P. indutum*, *P. pilosum*, and *P. tovarii*. Four species, *P. bicolor*, *P. brachyspermum*, *P. medium*, and *P. ruprechtianum*, are gathered in a clade (bs = 1) supported by the shape of the floret; all of them have obconical florets (13), rather than a terete to fusiform floret. *Piptochaetium brachyspermum* and *P. medium* are distinguished by the absence of macrohairs in the crown (24; bs = 1). Only *P. medium* has a wide floret with respect to its length (28, Cialdella & Arriaga, 1998: fig. 8B).

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DISCUSSION

Piptochaetium is a monophyletic genus clearly defined by reproductive characters related with lemma and palea structures (Fig. 3). The origin of *Piptochaetium* was supposed to be in North America according to Thomasson (1978a, 1980), who related this genus with *Berriochloa* Elias as its ancestor. This fossil grass was first characterized by Elias in 1932. Thomasson (1978a, b, 1985) found some similarities between *Piptochaetium* and *Berriochloa* based on floret shape, which can be cylindrical, obovoid, obconical, or lens-shaped in both genera. Although he emphasized similarities between epidermal patterns of the lemma, *Berriochloa*, *Piptochaetium*, and *Hesperostipa* (treated as *Stipa* sect. *Hesperostipa* by Thomasson) share a similar lemma epidermis with long fundamental cells with sinuous sidewalls (Thomasson, 1978a, b, 1982). This study shows *Hesperostipa* to be more closely related to *Piptochaetium* than *Nassella*. A more comprehensive evaluation of the relationship of *Piptochaetium* to other genera in the tribe requires a more inclusive study.

Within *Piptochaetium*, species were grouped in two sections: *Podopogon* and *Piptochaetium* (Table 1) according to the revision carried out by Parodi (1944) and as later accepted by Valencia and Costas (1968), Sánchez Vega (1991), and Cialdella and Arriaga (1998).

As suggested by cladistic analysis, *Piptochaetium* sect. *Podopogon* is not a natural entity. Consequently, infrageneric ranks cannot be supported. The species traditionally included in *Piptochaetium* sect. *Piptochaetium* (Parodi, 1944), with the exception of *P. fimbriatum* and *P. pringlei*, were assembled in a monophyletic group, here informally called the Obovoid group, also including *P. brevicalyx*. This clade is supported by two synapomorphies: a deciduous awn and obovoid florets. The Obovoid clade shares other synapomorphies with three North American species: a short callus with *P. angustifolium* and a short and blunt callus with *P. fimbriatum* and *P. seleri*. Short and blunt calluses are derived states within the genus, while acute and long calluses are plesiomorphic states (Fig. 3). This agrees with Thomasson (1985), who found that all species of *Berriochloa*, regardless of the floret shape, always had an acute callus. He suggested that the evolution of the blunt callus in *Piptochaetium* is a post-Miocene event.

Transition in floret shape was observed by Thomasson (1978b) in fossils of *Berriochloa* in Nebraska. He found a change in the floret shape from the oldest to the youngest stratigraphic levels: cylindrical or cylindrical-fusiform shapes were found in the oldest levels, while the youngest levels presented all possible forms within the genus: cylindrical, cylindrical-fusiform, obovoid, as well as spheroid florets. The present study supports Thomasson's findings, showing that obconical, obovoid, and lens-shaped florets are always derived states (Fig. 3). Species with obconical florets form a olute crown toward the outside (23; bs = 1); and optimization of characters 9, 18, 19, 22, 25, and 29 is ambiguous on this clade. Relationships among species are not resolved within this clade. Only *P. brachyspermum* and *P. cabrerae* also have a revolute crown, a character that appears independently in these taxa.

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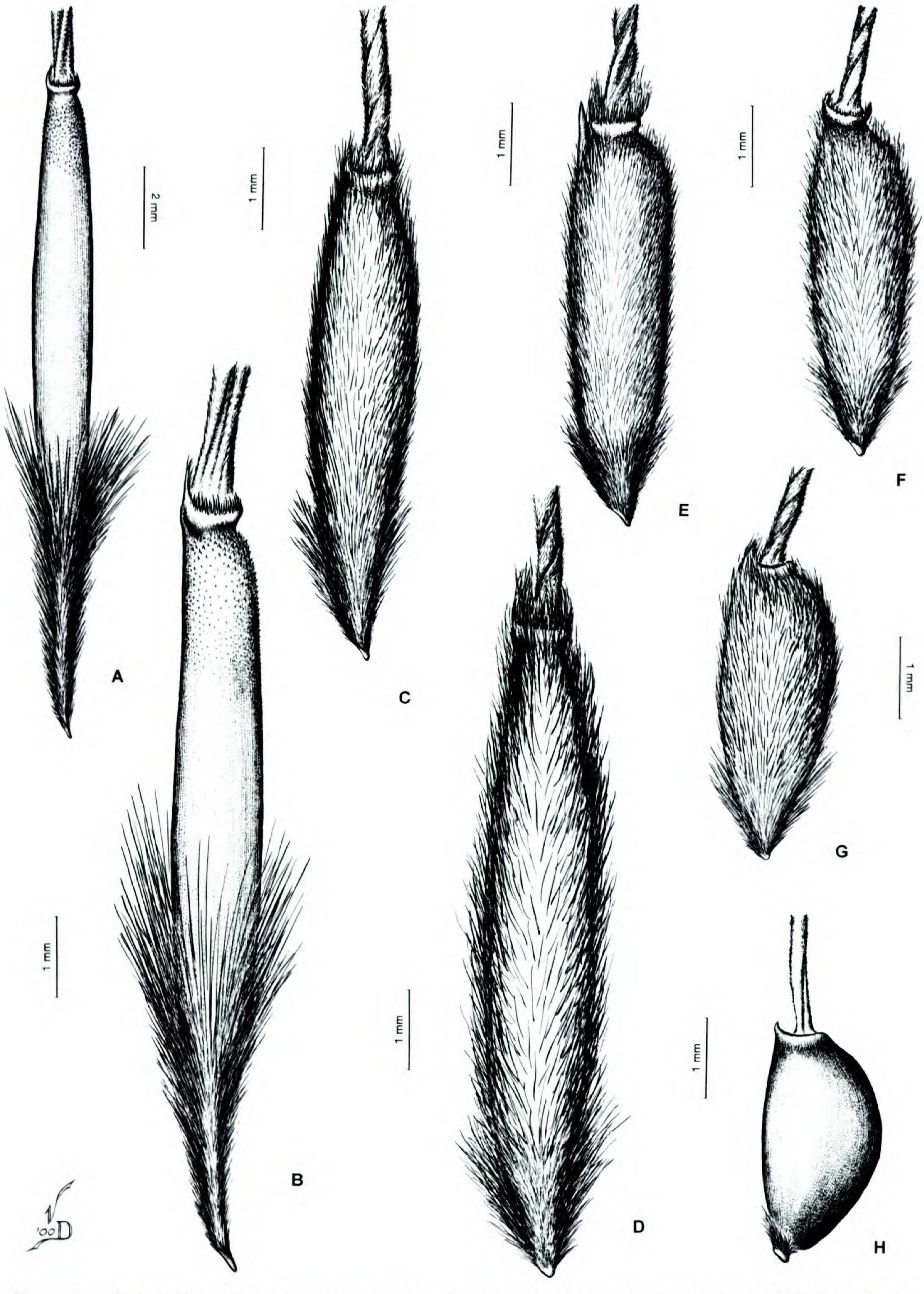
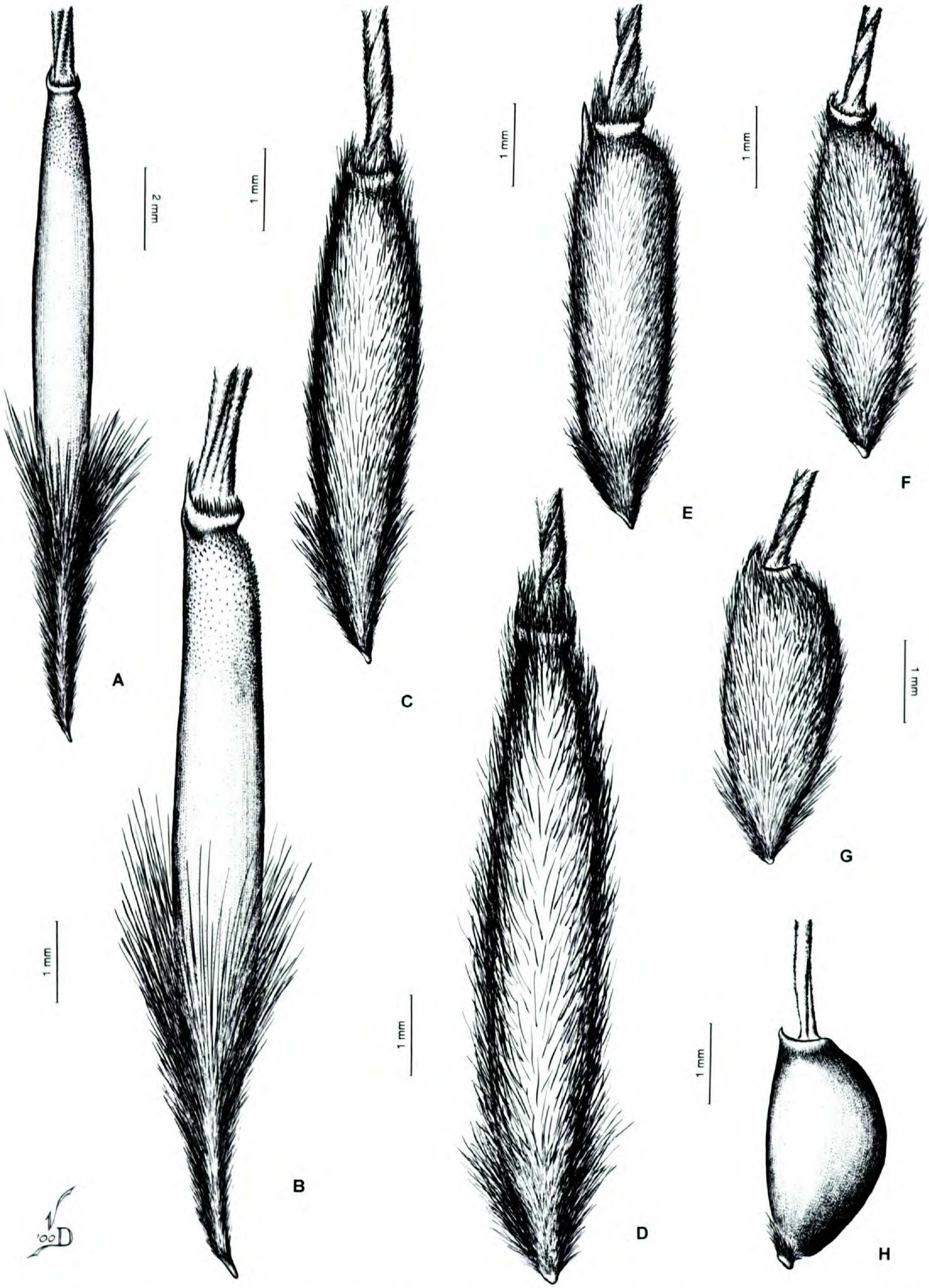


Figure 5. Florets of North American species of *Piptochaetium.*—A. *P. avenacioides* (*Fredholm 5725*). Note that the scale of this drawing is 2 mm. —B. *P. avenaceum* (*Harvey 1854*). —C. *P. virescens* (*King & Soderstrom 5151*). —D. *P. pringlei* (*Pringle 1410*). —E. *P. angustifolium* (*Matuda 29776 a*). —F. *P. seleri* (*Nee & Diggs 24775*). —G. *P. fimbriatum* (*Pringle 8595*). —H. *P. brevicalyx* (*Rzedowski 35863*).



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monophyletic group derived from species with cylindrical florets. Species with lens-shaped florets, *P. montevidense* and *P. panicoides*, are derived species within the Obovoid group (Fig. 3). The presence of papillae is another autapomorphy within this small monophyletic group of lens-shaped florets, which is only present in living grasses and never found in fossil taxa studied in this group of Stipeae (Thomasson, 1985).

Piptochaetium angustifolium, *P. fimbriatum*, and *P. seleri* (Fig. 5E, G, and F, respectively) have both plesiomorphic (persistent awns and cylindrical florets) and apomorphic (short and blunt callus) states. As shown by the phylogenetic analyses, these three North and Central American species are intermediate in the evolutionary trend through the Obovoid group.

Distribution patterns of species in *Piptochaetium* suggest that these species found new and different habitats to colonize in South America, with a consequent higher diversification than in the Northern Hemisphere. The monophyletic Obovoid group is mostly South American, except *P. brevicalyx* and *P. montevidense*, which are also present in Mexico, and *P. stipoides* var. *stipoides*, *P. setosum*, and *P. uruguense*, with disjunct distributions in North and South America (Fig. 4). According to Thomasson's suggestions (1980), disjunct species were first widespread along animal migration routes and, later, due to severe climatic fluctuation in the late Tertiary, their distribution became gradually reduced, resulting in relict islands in both hemispheres. Whether species with obovoid florets are derived from species with cylindrical florets in North America or in South America is difficult to determine, as there is no certain evidence for this fact.

INFRASPECIFIC LEVELS

Results from parsimony analyses showed a different origin for subspecies of *P. tovarii*, first recognized by Sánchez Vega (1991). Both subspecies of *P. tovarii* are separated in all cladistic analyses (see NONA and Pee-Wee results, Fig. 3). *Piptochaetium tovarii* subsp. *tovarii*, included herein within the *P. burkartianum* to *P. panicoides* clade, is characterized by the absence of prickles on the lemma surface, while *P. tovarii* var. *pilosa* (= *P. pilosum* herein) is the sister group of the *P. uruguense* to *P. stipoides* var. *echinulatum* clade and does have prickles and macrohairs. Based on these results, the study of type material, and the distribution of characters across the entire genus, there is no reason to keep these entities within the same species. Therefore, *P. tovarii* subsp. *pilosum* is elevated to the rank of species (see the taxonomic treatment herein).

Piptochaetium stipoides is included in the *P. cucullatum* to *P. stipoides* var. *echinulatum* clade (Fig. 4). Relationships between the two varieties of *P. stipoides* were not resolved as much as among the other species of the clade. A possible source of variation within this clade is the polymorphic state of *P. stipoides* var. *stipoides* for several characters principally related with the floret. Moreover, transitional shapes and epidermal characters of the lemma may be variable within a single specimen of this species.

TAXONOMIC TREATMENT

Piptochaetium J. Presl, Reliq. Haenk. 1: 222. 1830, nom. cons. *Urachne* Trin. sect. *Piptochaetium* (J. Presl) Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 22. 1842. TYPE: *Piptochaetium setifolium* J. Presl [= *P. panicoides* (Lam.) E. Desv.].

Podopogon Raf., Neogenyton: 4. 1825, nom. rejic. TYPE: *Stipa avenacea* L. (lectotype, designated by Clayton, 1983, not seen).

Caryochloa Spreng., Syst. Veg. 4(2): 22, 30. 1827, hom. illeg., non *Caryochloa* Trinius, 1826. TYPE: *Caryochloa montevidensis* Spreng.

Caespitose, perennial plants. *Culms* herbaceous, unbranched above, erect or somewhat decumbent, terete or slightly flattened, longitudinally striate, glabrous; young shoots intravaginal. *Nodes* compressed, occasionally thickened, the basal nodes slightly geniculate. *Leaf sheaths* generally longer than the internodes at the base, becoming shorter toward the apex. *Ligules* membranous, blunt, usually unfringed. *Leaf blades* linear, convolute to flat, longitudinally striate, frequently glabrous. *Inflorescence* a panicle with branches densely to loosely flowered. *Spikelets* fusiform, laterally compressed to terete, usually long pedicellate, the pedicels unequal in length, generally in pairs, rarely alone toward the apex of the panicle. *Flowers* cleistogamous or chasmogamous. *Glumes* two, persistent, subequal, usually longer than the floret, membranous, lanceolate, acuminate, 3- to 7(8)-nerved, glabrous. *Florets* easily deciduous, terete to laterally compressed. *Lemma* indurate, awned, longitudinally striate, generally with epidermal appendages; lemma margins involute, fitting into the longitudinal groove of the palea; lemma apex fused in a crown, frequently contracted to the base of the awn and with different epidermal appendages. *Awn* usually twice-geniculate, twisted and hispid on the basal portion, straight and shortly scabrous toward the apex, deciduous or persistent. *Callus* acute, subacute or blunt and obliquely truncate, usually hairy, rarely glabrous or subglabrous. *Palea* laterally compressed, monophyletic group derived from species with cylindrical florets. Species with lens-shaped florets, *P. montevidense* and *P. panicoides*, are derived species within the Obovoid group (Fig. 3). The presence of papillae is another autapomorphy within this small monophyletic group of lens-shaped florets, which is only present in living grasses and never found in fossil taxa studied in this group of Stipeae (Thomasson, 1985).

Piptochaetium angustifolium, *P. fimbriatum*, and *P. seleri* (Fig. 5E, G, and F, respectively) have both plesiomorphic (persistent awns and cylindrical florets) and apomorphic (short and blunt callus) states. As shown by the phylogenetic analyses, these three North and Central American species are intermediate in the evolutionary trend through the Obovoid group.

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KEY TO THE SPECIES OF *PIPTOCHAETIUM*

1a. Florets terete, fusiform or obconical, occasionally fusiform, slightly obovoid; awn robust and persistent; callus usually acute or subacute, rarely blunt.

2a. Lemma glabrous.

3a. Lemma with hooks all over surface, decreasing in density toward the callus and the crown .... 10. *P. cabrerai*

3b. Lemma with hooks and prickles on the upper portion.

4a. Lemma with inconspicuous hooks .... 25. *P. palustre*

4b. Lemma with hooks and prickles always conspicuous.

5a. Floret terete, not gibbous, slightly narrowed below the crown, (6–)9–20 mm long, 1–1.5 mm wide.

6a. Lower glume 7(8)-nerved; glumes 20–26(–35) mm long; lemma surface dull, with inconspicuous longitudinal striae .... 16. *P. hackelii*

6b. Lower glume 3(4)-nerved; glumes 15–23 mm long; lemma surface shiny, with conspicuous longitudinal striae.

7a. Floret (14–)15–20 mm long .... 5. *P. avenacioides*

7b. Floret (7–)9–12(–13) mm long .... 24. *P. napostaense*

5b. Floret fusiform, slightly gibbous, or obconical, strongly narrowed below the crown, (3.5–)7.5–11.5(–12) mm long, (0.8–)1.2–2 mm diam.

8a. Floret fusiform.

9a. Floret 1.2–1.5 mm wide; lemma with hooks and prickles only below the crown; callus 3.5–4.8 mm long, occasionally shorter .... 12. *P. confusum*

9b. Floret 1 mm wide; lemma with hooks and prickles on the distal half of the lemma; callus 2–3 mm long .... 4. *P. avenaceum*

8b. Floret obconical.

10a. Crown with ascending macrohairs up to 0.6 mm long, conspicuously exceeding the crown in length, sometimes also with a few hooks and prickles.

11a. Callus 1–2 mm long; floret (3.5–)4.5–6(–7) mm long .... 6. *P. bicolor*

11b. Callus 2.5–4 mm long; floret (5.5–)7.5–9.5 mm long .... 29. *P. ruprechtianum*

10b. Crown without macrohairs, with hooks and prickles up to 0.2 mm long, slightly longer than the crown.

12a. Crown 0.5–0.7 mm diam.; callus 1.2–1.5 mm long; floret (1.2–)1.5–2 mm wide .... 22. *P. medium*

12b. Crown 0.8–1 mm diam.; callus 1.9–2 mm long; floret 1.2–1.5 mm wide .... 7. *P. brachyspermum*

2b. Lemma with macrohairs densely disposed all over surface.

13a. Callus sharp and narrow.

14a. Inflorescence 3–9 cm long, with 4 to 15 spikelets; spikelets 9–13.5 mm long; Bolivia and Argentina .... 18. *P. indutum*

14b. Inflorescence longer, 10–30 cm long, with 15 to 80 spikelets; spikelets 5–10 mm long.

15a. Lower glume shorter than the floret; upper glume as long as the floret; Brazil .... 1. *P. alpinum*

15b. Both glumes longer than the floret.

16a. Plants 0.25–0.65 m long; peduncles 8–11.5 cm long; panicles with 15 to 22 spikelets; Peru .... 30. *P. sagasteguii*

16b. Plants 0.70–1.30 m long; peduncles 40–44 cm long; panicles with 25 to 80 spikelets; Mexico, Guatemala, and Venezuela .... 36. *P. virescens*

13b. Callus subacute or blunt, always broad.

17a. Lemma smooth, sometimes a very few hooks present near the crown.

18a. Floret 7–10 mm long; callus subacute .... 28. *P. pringlei*

18b. Floret 3.5–5 mm long; callus blunt .... 15. *P. fimbriatum*

17b. Lemma longitudinally striate, with hooks and prickles all over surface.

19a. Macrohairs of the lemma, including those of the crown, 1 mm long; floret fusiform .... 3. *P. angustifolium*

19b. Macrohairs of the lemma, including those of the crown, 0.5 mm long; floret terete, slightly obovoid.

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          8b. Floret obconical.

            10a. Crown with ascending macrohairs up to 0.6 mm long, conspicuously exceeding the crown in length, sometimes also with a few hooks and prickles.

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20a. Peduncles 5–14 cm long; inflorescences 3–6.5 cm long, dense; Peru 14. *P. featherstonei*

20b. Peduncles 22–26 cm long; inflorescences 7–22 cm long, loose, not dense; Mexico and Guatemala 31. *P. seleri*

1b. Florets obovoid or lens-shaped; awn weak and deciduous; callus blunt.

21a. Lemma with many macrohairs.

22a. Macrohairs of the lemma up to 4 mm long, conspicuously longer than the crown 20. *P. lasianthum*

22b. Macrohairs of the lemma up to 2 mm long, the upper hairs slightly longer than the crown 27. *P. pilosum*

21b. Lemma glabrous.

23a. Awn cone-shaped, base as wide as the crown (0.9–1 mm), glabrous, or occasionally with very few hairs 13. *P. cucullatum*

23b. Awn thread-like, shortly hispid, minutely scabrous toward the apex.

24a. Crown 1–1.8 mm diam., not contracted toward the base of the awn.

25a. Callus glabrous, or with few short hairs as long as the callus.

26a. Hooks of the lemma inconspicuously pointed, densely disposed all over the surface, decreasing in size and quantity toward the callus and near the crown 11. *P. calvescens*

26b. Lemma with very few hooks, these confined to the distal part toward the crown 21. *P. lejopodum*

25b. Callus densely hairy, the hairs exceeding the callus.

27a. Hairs of the callus longer than the floret 19. *P. jubatum*

27b. Hairs of the callus one-third or half as long as the floret.

28a. Lemma with prickles partially covered by the edges of adjacent epidermal cells, generally in groups of 2 or 3, uniformly disposed all over the lemma surface, the biggest ones on the middle portion of the floret 33b. *P. stipoides* var. *echinulatum*

28b. Lemma with hooks and prickles not covered by the adjacent cells, uniformly disposed on the distal half of the floret, or lemma without epidermal appendages 33a. *P. stipoides* var. *stipoides*

24b. Crown 0.4–0.6(–0.9) mm diam., contracted toward the base of the awn.

29a. Lemma with hooks and prickles, densely and uniformly disposed on the distal ¾ of the floret; papillae absent.

30a. Floret globose, sometimes slightly compressed laterally, (1.8–)2.4–3(–3.5) mm long, 0.8–1.2 mm diam.; Paraguay, Uruguay, and northern Argentina 35. *P. uruguense*

30b. Floret elongate and conspicuously laterally compressed, (2.5–)3.8–4(–5) mm long, 1–2 mm wide; Chile 2. *P. angolense*

29b. Lemma with papillae or with hooks and prickles only below the crown, or lemma without epidermal appendages.

31a. Crown revolute toward the outside 33a. *P. stipoides* var. *stipoides*

31b. Crown not revolute.

32a. Floret lens-shaped, conspicuously laterally compressed; lemma and crown with or without papillae.

33a. Lemma with papillae dense and uniformly disposed, decreasing in size and density toward the crown and the callus 23. *P. montevidense*

33b. Lemma without papillae, or confined to the region near the crown, on the dorsal side of the floret 26. *P. panicoides*

32b. Floret globose to slightly compressed, obovoid, or obconical; lemma and crown with or without hooks, prickles, and macrohairs.

34a. Lemma with a few hooks toward the crown 32. *P. setosum*

34b. Lemma without epidermal appendages.

35a. Leaf blades glabrous; floret 2.2–2.5 mm long; callus hairy, the upper hairs ½ the length of the floret 9. *P. burkartianum*

35b. Leaf blades hispid on both surfaces, sometimes abaxially glabrous; floret 2.5–3.5 mm long; callus with or without short hairs, the hairs equaling the length of the callus.

36a. Floret obovoid, not gibbous, 0.8–1.2 mm wide 34. *P. tovarii*

36b. Floret conspicuously gibbous, 1.5–1.9 mm wide.

37a. Glumes exceeding the length of the floret; lemma dull, with conspicuous longitudinal striae; callus 0.4–0.5 mm long, crown with 1 or 2 rows of hooks and prickles on margin 17. *P. hirtum*

37b. Glumes as long as or slightly shorter than the floret; lemma shiny, smooth; callus 0.15–0.25 mm long; crown without epidermal appendages 8. *P. brevicalyx*

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1. **Piptochaetium alpinum** L. B. Smith, Phytologia 22: 89. 1971. TYPE: Brazil. Santa Catarina: Bom Jardim da Serra, Fazenda da Laranja, 1400 m, *Reitz & Klein 7710* (holotype, US not seen; isotype, HBR not seen).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, up to 1400 m elevation.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

2. **Piptochaetium angolense** Philippi, Anales Univ. Chile 93: 734. 1896. TYPE: Chile. "Angol, Nov. 1887," *Philippi s.n.* (holotype, SGO 057397!).

Distribution. Endemic to central Chile (IV Región).

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

3. **Piptochaetium angustifolium** (Hitchcock) Valencia & Costas, Bol. Soc. Argent. Bot. 12: 177. 1968. *Stipa angustifolia* Hitchc., Contr. U.S. Natl. Herb. 24: 246. 1925. TYPE: Mexico. Coahuila: on summit slope of Sierra de La Puebla in sight of Saltillo, 25 July 1905, *Palmer 726* (holotype, US 570290 not seen; isotypes, BAA Herb. Parodi 2955!, MO!, US 993385 not seen, US 906342 not seen). Figures 2D, 5E.

Plants perennial. *Culms* 10–30 cm tall, glabrous; nodes 2, compressed, glabrous to sparingly pubescent; internodes 3.5–4.5 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 3–4 cm long, glabrous. *Ligules* 1–2 cm long, blunt, margins entire, glabrous. *Leaf blades* linear, convolute, 9–10(–20) cm long, 0.5–0.6 mm wide, longitudinally striate, glabrous. *Peduncles* terete, slightly flattened, 7–10 cm long, longitudinally striate, glabrous. *Inflorescences* 6.5–7.5 cm long, few-flowered (8 to 18 spikelets), with branches loosely disposed; pedicels 2–7 mm long, scabrous. *Spikelets* fusiform, 6–6.5 mm long, 1 mm diam. *Glumes* longer than the floret, subequal, 6–6.5 mm long, shortly acuminate, 5-nerved, greenish, hyaline toward the margins. *Floret* fusiform, 4.5–5 mm long, 0.9–1 mm diam. *Lemma* 4.5–5 mm long, contracted below the crown, longitudinally striate, densely pilose, with macrohairs 1 mm long, hooks and prickles all over surface; crown contracted at the base of the awn, 0.4–0.5 mm diam., straight, not revolute, with densely disposed prickles and macrohairs, the latter 1 mm long, persistent; callus 0.6–1 mm long, subacute, densely pilose, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 10–11 mm long, persistent, scabrous along length. *Palea* 4 mm long. *Lodicules* 2, 1 mm long, blunt. *Caryopsis* not seen.

Distribution. This species is known only from northeastern and eastern Mexico, in the states of Coahuila, Nuevo León, and Mexico, up to 3500 m.

Additional specimens examined. MEXICO. **México:** C. Pelon de Ñado, 2700–3500 m, *Matuda et al. 29776* (US). **Nuevo León:** Hacienda Vista Hermosa, 35 mi. S of Monterrey, 810 m, 25 June 1939, *Harvey 1038* (US).

Piptochaetium angustifolium is similar to *P. featherstonei* and *P. seleri*, but these species differ in having short, 0.5 mm, macrohairs on the lemma and crown, and a terete, slightly obovoid floret.

4. **Piptochaetium avenaceum** (L.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 229. 1944. *Stipa avenacea* L., Sp. Pl. 1: 78. 1753. TYPE: U.S.A. Virginia: *Clayton 621* (lectotype, designated by Clayton (1983), LINN-94.5 not seen; isolectotype, BM not seen). Figures 2C, 5B.

Stipa barbata Michx., Fl. Bor.-Amer. 1: 53. 1803, nom. illeg., non *Stipa barbata* Desf., Fl. Atlant. 1: 97. 1798. *Stipa virginica* Pers., Syn. Pl. 1: 99. 1805. *Podopogon barbatus* Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. TYPE: U.S.A. "In sylvis Virginiae Carolinae," *Michaux s.n.* (holotype, P not seen; isotype, US not seen).

Stipa avenacea var. *bicolor* Eaton & J. Wright, Man. Bot. (ed. 8): 444. 1848. TYPE: "United States of America" (not located).

Stipa leiantha Hitchc., Contr. U.S. Natl. Herb. 24: 236. 1925. *Piptochaetium leianthum* (Hitchc.) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico. Puebla: 2600 m, *Hitchcock 6489* (holotype, US 993443 not seen).

Piptochaetium avenacellum Barkworth, Syst. Bot. 13: 196. 1988. TYPE: Mexico. Tamaulipas: 4 km W of Miquihauan, 23°42′N, 99°45′W, on limestone ridges in open pine forest, 3110 m, 4 Aug. 1941, *Stanford et al. 645A* (holotype, US not seen; isotype, MO not seen).

Plants perennial. *Culms* (30–)50–80 cm tall, glabrous; nodes 2–3, yellowish to reddish, compressed, glabrous; internodes 5–25 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, (4–)6–16 cm long, glabrous. *Ligules* 2–3 mm long, subacute to blunt, margins entire, glabrous. *Leaf blades* linear, convolute, occasionally flat, 8–30 cm long, 0.8–0.9 mm wide, adaxial side conspicuously striate, glabrous or scabrous, margins shortly scabrous. *Peduncles* terete, slightly flattened, 8–10 cm long, longitudinally striate, gla-

1. Piptochaetium alpinum L. B. Smith, Phytologia 22: 89. 1971. TYPE: Brazil. Santa Catarina: Bom Jardim da Serra, Fazenda da Laranja, 1400 m, *Reitz & Klein 7710* (holotype, US not seen; isotype, HBR not seen).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, up to 1400 m elevation.

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Plants perennial. *Culms* 10–30 cm tall, glabrous; nodes 2, compressed, glabrous to sparingly pubescent; internodes 3.5–4.5 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 3–4 cm long, glabrous. *Ligules* 1–2 cm long, blunt, margins entire, glabrous. *Leaf blades* linear, convolute, 9–10(–20) cm long, 0.5–0.6 mm wide, longitudinally striate, glabrous. *Peduncles* terete, slightly flattened, 7–10 cm long, longitudinally striate, glabrous. *Inflorescences* 6.5–7.5 cm long, few-flowered (8 to 18 spikelets), with branches loosely disposed; pedicels 2–7 mm long, scabrous. *Spikelets* fusiform, 6–6.5 mm long, 1 mm diam. *Glumes* longer than the floret, subequal, 6–6.5 mm long, shortly acuminate, 5-nerved, greenish, hyaline toward the margins. *Floret* fusiform, 4.5–5 mm long, 0.9–1 mm diam. *Lemma* 4.5–5 mm long, contracted below the crown, longitudinally striate, densely pilose, with macrohairs 1 mm long, hooks and prickles all over surface; crown contracted at the base of the awn, 0.4–0.5 mm diam., straight, not revolute, with densely disposed prickles and macrohairs, the latter 1 mm long, persistent; callus 0.6–1 mm long, subacute, densely pilose, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 10–11 mm long, persistent, scabrous along length. *Palea* 4 mm long. *Lodicules* 2, 1 mm long, blunt. *Caryopsis* not seen.

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Plants perennial. *Culms* (30–)50–80 cm tall, glabrous; nodes 2–3, yellowish to reddish, compressed, glabrous; internodes 5–25 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, (4–)6–16 cm long, glabrous. *Ligules* 2–3 mm long, subacute to blunt, margins entire, glabrous. *Leaf blades* linear, convolute, occasionally flat, 8–30 cm long, 0.8–0.9 mm wide, adaxial side conspicuously striate, glabrous or scabrous, margins shortly scabrous. *Peduncles* terete, slightly flattened, 8–10 cm long, longitudinally striate, glabrous. *Inflorescences* 15–22 cm long, few-flowered (10 to 15(–25) spikelets), with branches loosely disposed; pedicels flattened, 1.5–5 cm long, hispid. *Spikelets* fusiform, 10–12 mm long, 1–1.2 mm diam. *Glumes* subequal, longer than the floret, 10–12(–15) mm long, acute, lower glume 3(5)-nerved, upper glume 5-nerved. *Floret* terete-fusiform, slightly compressed, (7–)9–12(–13) mm long, 1 mm diam. *Lemma* contracted below the crown, 9–12(–13) mm long, thinly striate, with hooks and prickles toward the distal portion (1/3–2/3 of the surface); crown contracted at the base of the awn, straight, not revolute, 0.5–0.6 mm diam., with prickles and macrohairs up to 0.5 mm long, occasionally up to 1 mm long; callus ca. 2 mm long, sharp, hairy, the upper macrohairs reaching ⅓–½ the length of the floret; awn bigeniculate, 5–7 cm long, persistent, hispid, scabrous toward the apex. *Palea* 7–8 mm long. *Lodicules* 2, 1.5 mm long, acute. *Caryopsis* terete, 5.5–6 mm long, 0.5–0.6 mm diam.; hilum linear; embryo ⅕ the length of the caryopsis.

Chromosome numbers. 2*n* = 22, 28 (Gould, 1958, as *Stipa avenacea* L.); n = 11 (Valencia & Costas, 1968).

Distribution. Widespread in the eastern and southern United States and northeastern Mexico.

Additional specimens examined. U.S.A. **Alabama:** Marshall Co., margin of a woodland, along Alabama 240, about 10 mi. E of Morgan City, *Henderson 91–3* (MO); Lee Co., Auburn, *Earle & Baker s.n.* (US 344773). **Arkansas:** Garland Co., 30 Apr. 1939, *Demaree 19003* (US); Coastal Plain Region, *Demaree 63483* (MO). **Connecticut:** New Haven Co., dry ledgy places toward summit of Mt. Carmel, *Weatherby 5831* (US). **Florida:** Wakulla Co., St. Marks Wildlife Refuge, *Godfrey 67795* (US); Highlands Co., waste area just W of Sebring, *Deam 64413* (US); Gainesville, *Garber s.n.* (US 992485). **Georgia:** Ben Hill Co., 16.3 mi. ENE of Fitzgerald, *Faircloth 5079* (MO); Glynn Co., N end of Jekyll Island, *Strong 1342* (US); Walker Co., near summit of ridge near Maddox Gap, between Villanow and La Fayette, *Cronquist 4432* (US). **Indiana:** N side of the Pidgeon River about 3 mi. SE of Mongo, *Deam 40704* (US). **Louisiana:** Pipeline off La. 507, 3 mi. W of Bienville, *Larrick 249* (BAA); roadside about 2 mi. NE of Mansfield, *Thieret 28558* (US). **Maryland:** region of Marlboro, *Hitchcock 12616* (US). **Massachusetts:** Barnstable Co., *Hoffmann s.n.* (MO); Tisbuty, *Seymour 1060* (US); just E of hwy. 28, near junction with hwy. 138, Blue Hill Reservation, SE of Boston, *Reeder & Reeder 233* (US). **Michigan:** 6 mi. W of Richland at Spring Brook and railroad, *Harvey 1764* (SI); Kalamazoo Co., Sect. 36, 2 mi. S of Alamo, *Harvey 1854* (BAA, US). **Mississippi:** Lowndes Co., just W of Mayhew junction on ridge, *McDaniel 1811* (MO); Wayne Co., Bucatunna, *Jacob 815* (US). **New Jersey:** near Jenkins, Wharton State Forest, Pine Barrens, *Harkins 809* (MO); Atlantic Co., *Chase 7312* (US). **New York:** Eastport, Long Island, *Chase 7401* (US). **North Carolina:** Wake Co., Lake Johnson, 4 mi. SW of Raleigh, *Godfrey 3686* (US); Durham Co., wooded slope, *Simpson s.n.* (US 2479778). **Oklahoma:** Le Flore Co., near state line on hwy. 63, E of Big Cedar, *Waterfall 14854* (US). **Pennsylvania:** s.l., *Scribner 266* (US). **Rhode Island:** Providence Co., *Collins s.n.* (US 1912039). **South Carolina:** Laurens Co., side of U.S. 276, just SE of Ora, *Iltis 23032* (MO); Horry Co., S of Myrtle Beach, *Griscom 16409* (US); McCormick Co., 1 mi. NE of Savannah River on SC hwy. 28, *Bozeman & Radford 8842* (US). **Tennessee:** Marion Co., 9 mi. SE of Tracy City, *Kral 46479* (MO); Roane Co., last slope of Cumberland Plateau, W of Rockwood, *Weatherby 6234* (US). **Texas:** Jasper Co., 8 mi. SE of Jasper, hwy. 190, *Shinners 7029* (SI); Shelby Co., sandy scrub oak land 7 mi. S of Center, *Correll 16170* (US). **Virginia:** Accomac Co., Chincoteague Island, *Gleason 8537* (US); Hampton, dry open woods, *Miller Jr. s.n.* (US 646829). **West Virginia:** on wooded hillside near Reymon Memorial farm, Wardensville, *Berkley 1579* (MO). MEXICO. **Tamaulipas:** 3 mi. N of Miquihauana, *Stanford et al. 2482* (US, paratype of *Piptochaetium avenacellum*).

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5. **Piptochaetium avenacioides** (Nash) Valencia & Costas, Bol. Soc. Argent. Bot. 12: 175. 1968. *Stipa avenacioides* Nash, Bull. Torrey Bot. Club 22: 423. 1895. TYPE: U.S.A. Florida: Lake Co., in pine lands near Cassia, 16/30 June 1895, *Nash 2051* (holotype, NY not seen; isotypes, BAA!, MO!, US!). Figure 5A.

Plants perennial. *Culms* 0.70–1.20 m tall, glabrous or pubescent below the basal nodes; nodes yellowish, glabrous; internodes 15–25 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 7–20 cm long, glabrous. *Ligules* 1–3 mm long, blunt or acute, margins entire, glabrous. *Leaf blades* linear, convolute, 15–30 cm long, 1 mm wide, longitudinally striate, glabrous. *Peduncles* terete, 22–25 cm long, longitudinally striate, glabrous. *Inflorescences* 10–30 cm long, few- to many-flowered (10 to 50 spikelets), with branches loosely disposed; pedicels 1.5–2 cm long, scabrous. *Spikelets* fusiform, 18–22 mm long, 1–2 mm diam. *Glumes* longer than the floret, 18–22 mm long, acuminate, (3)5-nerved. *Floret* terete, (14–)15–20 mm long, 1–1.2 mm diam. *Lemma* 15–20 mm long, contracted below the crown, longitudinally striate, with brous. *Inflorescences* 15–22 cm long, few-flowered (10 to 15(–25) spikelets), with branches loosely disposed; pedicels flattened, 1.5–5 cm long, hispid. *Spikelets* fusiform, 10–12 mm long, 1–1.2 mm diam. *Glumes* subequal, longer than the floret, 10–12(–15) mm long, acute, lower glume 3(5)-nerved, upper glume 5-nerved. *Floret* terete-fusiform, slightly compressed, (7–)9–12(–13) mm long, 1 mm diam. *Lemma* contracted below the crown, 9–12(–13) mm long, thinly striate, with hooks and prickles toward the distal portion (1/3–2/3 of the surface); crown contracted at the base of the awn, straight, not revolute, 0.5–0.6 mm diam., with prickles and macrohairs up to 0.5 mm long, occasionally up to 1 mm long; callus ca. 2 mm long, sharp, hairy, the upper macrohairs reaching ⅓–½ the length of the floret; awn bigeniculate, 5–7 cm long, persistent, hispid, scabrous toward the apex. *Palea* 7–8 mm long. *Lodicules* 2, 1.5 mm long, acute. *Caryopsis* terete, 5.5–6 mm long, 0.5–0.6 mm diam.; hilum linear; embryo ⅕ the length of the caryopsis.

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Distribution and ecology. Only known from the United States, in Florida. This species grows in dry and sandy places.

Additional specimens examined. U.S.A. **Florida:** Brevard Co., *Fredholm 5725* (BAA, MO, US); Eau Gallie, *Curtiss 5834* (MO, US); Orange Co., Mermiack, *Baker 115* (US); Manatel Co., Palma Sola, *Tracy 7031* (MO, US); Duval Co., *Fredholm 5092* (US); W of Tavares, *Hitchcock 812* (US); Braidentown, *Hitchcock 967* (US); s.l., *Dowell 7309* (BAA, US); Orange Co., Clarcona, *Meislahn 191* (US).

6. Piptochaetium bicolor (Vahl) E. Desvaux, Fl. Chil. 6: 273. 1853. *Stipa bicolor* Vahl, Symb. Bot. 5(2): 24. 1791. *Oryzopsis bicolor* (Vahl) Speg., Anales Mus. Nac. Montevideo 4(2): 6. 1901. *Piptochaetium bicolor* var. *typicum* Parodi, Revista Mus. La Plata 6(25): 252. 1944, nom. inval. TYPE: Uruguay. "Habitat in Brasiliae Monte Video. *Dn. Thouin,*" Herb. Vahl, IDC microfiche photo Vahl, nr. 73 III, 4–5 (holotype, C!).

Stipa intermedia Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 26. 1842. TYPE: Brazil. "Brasilia meridionalis," *Sellow δ 784* (holotype, LE not seen; isotypes, US!, B not seen).

Stipa megalantha Steud., Syn. Pl. Glumac. 1: 124. 1854. TYPE: Chile. Valparaíso, Concon, Nov. 1829, *Herb. Steudel* (holotype, P!).

Oryzopsis bicolor (Vahl) Speg. var. *minor* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. *Piptochaetium bicolor* (Vahl) E. Desv. var. *minor* (Speg.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 256. 1944. TYPE: Argentina. Buenos Aires: Bavio, Estancia Elizalde, *Spegazzini s.n.* (holotype, LPS 12513! sheet A; isotype, LPS 12513! sheet B).

Distribution. Central Chile, in V Región, western and southern Uruguay in the departments of Canelones, Florida, Montevideo, and San José, and central eastern Argentina in the provinces of Buenos Aires and Entre Ríos.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

7. Piptochaetium brachyspermum (Spegazzini) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 241. 1944. *Oryzopsis napostaensis* Speg. var. *brachysperma* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Carmen de Patagones, *Spegazzini 42 b* (holotype, LPS 2471!).

Distribution. Endemic to Argentina, where it is only known from the southern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

8. Piptochaetium brevicalyx (E. Fournier) Ricker, Contr. U.S. Natl. Herb. 17: 286. 1918. *Stipa brevicalyx* E. Fourn., Mexic. Pl. 2: 150. 1886. TYPE: Mexico. San Luis Potosí: cerca de San Luis Potosí, 6000–8000 ft., 1878, *Parry & Palmer 959* (holotype, US not seen; isotypes, BAA!, K not seen, MO not seen, NY not seen). Figures 1A, 2A, 5H.

Piptochaetium brevicalyx (E. Fourn.) Ricker subsp. *flexuosum* Barkworth, Syst. Bot. 13: 200. 1988. TYPE: Mexico. Durango: 65–75 km W of Durango City on road to La Flor, 2620 m elevation, *Breedlove 44215* (holotype, CAS 622475 not seen).

Plants perennial. *Culms* (6–)10–50 cm tall; nodes 3 or 4, compressed, reddish, glabrous; internodes 2–12 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 2–5 cm long, glabrous to scabrous. *Ligules* 0.6–1.2 mm long, blunt to subacute, margins entire or fringed, glabrous. *Leaf blades* linear, convolute or flat, 5–30 cm long, 0.6–1.2 mm wide, glabrous or hispid. *Peduncles* terete, 2.5–7 cm long, longitudinally striate, glabrous. *Inflorescences* 3–10 cm long, few-flowered (5 to 20 spikelets), with branches densely disposed; pedicels 2–8 mm long, glabrous or hispid. *Spikelets* globose, 2.5–3.5 mm long, 1.5–1.7 mm diam. *Glumes* subequal, shortly acuminate, violet-colored, hyaline toward the margins, 5- or 7-nerved; lower glume slightly shorter than the floret, 2.4–3.3 mm long; upper glume shorter than or as long as the floret, 2.4–3.5 mm long. *Floret* globose, slightly compressed, gibbous, 2.5–3.5 mm long, 1.5–1.9 mm wide. *Lemma* contracted below the crown, 2.5–3.5 mm long, smooth, shiny, without epidermal appendages; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.5–0.7 mm diam., without epidermal appendages; callus 0.15–0.25 mm long, blunt, obliquely truncate, with few, occasionally many, short hairs; awn slightly geniculate to almost straight, 6–18 mm long, hispid, scabrous toward the apex, deciduous. *Palea* 2.5–3.7 mm long. Lodicules 2, 1 mm long, acute. *Caryopsis* not seen.

Distribution. Central Mexico, up to aproximately 3000 m.

Additional specimens examined. MEXICO. **Durango:** 5.3 km W of (Ejido) Los Mimbres turnoff, *Iltis et al. 214* (US); 41 km NE of El Salto, *Mick & Roe 87* (US! paratype small hooks on the distal portion (1/3–2/3 of the surface); crown contracted at the base of the awn, 0.6–0.7 mm diam., with hooks, prickles, and macrohairs 0.4–0.5 mm long, persistent; callus 6–8 mm long, acute, densely hairy; awn bigeniculate, persistent, 8–12 mm long, hispid at the basal portion, scabrous toward the apex. *Palea* 12 mm long. *Lodicules* 2, ca. 2.5 mm long, acute. *Caryopsis* not seen.

Distribution and ecology. Only known from the United States, in Florida. This species grows in dry and sandy places.

Additional specimens examined. U.S.A. **Florida:** Brevard Co., *Fredholm 5725* (BAA, MO, US); Eau Gallie, *Curtiss 5834* (MO, US); Orange Co., Mermiack, *Baker 115* (US); Manatel Co., Palma Sola, *Tracy 7031* (MO, US); Duval Co., *Fredholm 5092* (US); W of Tavares, *Hitchcock 812* (US); Braidentown, *Hitchcock 967* (US); s.l., *Dowell 7309* (BAA, US); Orange Co., Clarcona, *Meislahn 191* (US).

6. Piptochaetium bicolor (Vahl) E. Desvaux, Fl. Chil. 6: 273. 1853. *Stipa bicolor* Vahl, Symb. Bot. 5(2): 24. 1791. *Oryzopsis bicolor* (Vahl) Speg., Anales Mus. Nac. Montevideo 4(2): 6. 1901. *Piptochaetium bicolor* var. *typicum* Parodi, Revista Mus. La Plata 6(25): 252. 1944, nom. inval. TYPE: Uruguay. "Habitat in Brasiliae Monte Video. *Dn. Thouin,*" Herb. Vahl, IDC microfiche photo Vahl, nr. 73 III, 4–5 (holotype, C!).

Stipa intermedia Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 26. 1842. TYPE: Brazil. "Brasilia meridionalis," *Sellow δ 784* (holotype, LE not seen; isotypes, US!, B not seen).

Stipa megalantha Steud., Syn. Pl. Glumac. 1: 124. 1854. TYPE: Chile. Valparaíso, Concon, Nov. 1829, *Herb. Steudel* (holotype, P!).

Oryzopsis bicolor (Vahl) Speg. var. *minor* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. *Piptochaetium bicolor* (Vahl) E. Desv. var. *minor* (Speg.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 256. 1944. TYPE: Argentina. Buenos Aires: Bavio, Estancia Elizalde, *Spegazzini s.n.* (holotype, LPS 12513! sheet A; isotype, LPS 12513! sheet B).

Distribution. Central Chile, in V Región, western and southern Uruguay in the departments of Canelones, Florida, Montevideo, and San José, and central eastern Argentina in the provinces of Buenos Aires and Entre Ríos.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

7. Piptochaetium brachyspermum (Spegazzini) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 241. 1944. *Oryzopsis napostaensis* Speg. var. *brachysperma* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Carmen de Patagones, *Spegazzini 42 b* (holotype, LPS 2471!).

Distribution. Endemic to Argentina, where it is only known from the southern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

8. Piptochaetium brevicalyx (E. Fournier) Ricker, Contr. U.S. Natl. Herb. 17: 286. 1918. *Stipa brevicalyx* E. Fourn., Mexic. Pl. 2: 150. 1886. TYPE: Mexico. San Luis Potosí: cerca de San Luis Potosí, 6000–8000 ft., 1878, *Parry & Palmer 959* (holotype, US not seen; isotypes, BAA!, K not seen, MO not seen, NY not seen). Figures 1A, 2A, 5H.

Piptochaetium brevicalyx (E. Fourn.) Ricker subsp. *flexuosum* Barkworth, Syst. Bot. 13: 200. 1988. TYPE: Mexico. Durango: 65–75 km W of Durango City on road to La Flor, 2620 m elevation, *Breedlove 44215* (holotype, CAS 622475 not seen).

Plants perennial. *Culms* (6–)10–50 cm tall; nodes 3 or 4, compressed, reddish, glabrous; internodes 2–12 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 2–5 cm long, glabrous to scabrous. *Ligules* 0.6–1.2 mm long, blunt to subacute, margins entire or fringed, glabrous. *Leaf blades* linear, convolute or flat, 5–30 cm long, 0.6–1.2 mm wide, glabrous or hispid. *Peduncles* terete, 2.5–7 cm long, longitudinally striate, glabrous. *Inflorescences* 3–10 cm long, few-flowered (5 to 20 spikelets), with branches densely disposed; pedicels 2–8 mm long, glabrous or hispid. *Spikelets* globose, 2.5–3.5 mm long, 1.5–1.7 mm diam. *Glumes* subequal, shortly acuminate, violet-colored, hyaline toward the margins, 5- or 7-nerved; lower glume slightly shorter than the floret, 2.4–3.3 mm long; upper glume shorter than or as long as the floret, 2.4–3.5 mm long. *Floret* globose, slightly compressed, gibbous, 2.5–3.5 mm long, 1.5–1.9 mm wide. *Lemma* contracted below the crown, 2.5–3.5 mm long, smooth, shiny, without epidermal appendages; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.5–0.7 mm diam., without epidermal appendages; callus 0.15–0.25 mm long, blunt, obliquely truncate, with few, occasionally many, short hairs; awn slightly geniculate to almost straight, 6–18 mm long, hispid, scabrous toward the apex, deciduous. *Palea* 2.5–3.7 mm long. Lodicules 2, 1 mm long, acute. *Caryopsis* not seen.

Distribution. Central Mexico, up to aproximately 3000 m.

Additional specimens examined. MEXICO. **Durango:** 5.3 km W of (Ejido) Los Mimbres turnoff, *Iltis et al. 214* (US); 41 km NE of El Salto, *Mick & Roe 87* (US! paratype of *P. brevicalyx* subsp. *flexuosum*). **Guanajuato:** 10 km al sur de Ibarra, Ocampo, sobre la carretera a León, *Rzedowski 50768* (MEXU). **Hidalgo:** 8 km al noreste de Pachuca, sobre la carretera a Real del Monte, *Rzedowski 35863* (MEXU, XAL); Cerro Ventoso, above Pachuca, *Pringle 7606* (MEXU); in oak woods near Real del Monte, *Rose et al. 8680* (US); Pachuca, *Hitchcock 6733* (US). **México:** rocky roadcut, 27 mi. S of San Juan del Río, *Gould 9211* (US). **San Luis Potosí:** Cerro La Bolsa, W de Cerrito de Dolores, Mun. Villa de Arriaga, *Banda et al. 132* (CAS, MO); near Cerro Prieto, *Sohns 1535* (US). **Tlaxcala:** between San Cristóbal and Calpulalpan, *Sohns 553* (MEXU, US).

Piptochaetium brevicalyx is similar to *P. hirtum*: both species share the globose floret shape, the absence of epidermal appendages on the lemma, and generally few hairs on the callus. They can be recognized because *P. hirtum* presents conspicuous longitudinal striae on the dull lemma surface, 1 or 2 rows of hooks or prickles in the crown, and both glumes 5.5–6 mm, longer than the floret.

Barkworth (1988) recognized *Piptochaetium brevicalyx* subsp. *flexuosum* based on the relatively long and widespread branches of the inflorescences. Although there are specimens with dense or extended panicles, the difference between the length of the branches is slight, and, within the studied material, there are specimens with both types of inflorescences, such as *Banda et al. 132*.

9. Piptochaetium burkartianum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 291. 1944. TYPE: Argentina. Corrientes: San Martín, La Cruz, Nov. 1936, *Parodi 12329 1/2* (holotype, BAA!).

Distribution. Endemic to Argentina; only found in the eastern province of Corrientes, at the type locality.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

10. Piptochaetium cabrerae Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 243. 1944. TYPE: Argentina. Buenos Aires: Puan, Villa Iris, 7 Nov. 1940, *Parodi 13771* (holotype, BAA!).

Distribution. Endemic to Argentina; only collected in the southwestern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

11. Piptochaetium calvescens Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 278. 1944. TYPE: Argentina. Prov. Buenos Aires: Sierra Currumalán, 600 m s.m., 10 Nov. 1932, *Parodi 10343* (holotype, BAA!).

Distribution. Central and eastern Argentina in the province of Buenos Aires, and southern Uruguay in the department of Montevideo.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

12. Piptochaetium confusum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 246. 1944. TYPE: Argentina. Entre Ríos: Concordia, 3 Nov. 1921, *Parodi 3950* (holotype, BAA!).

Distribution and ecology. Uruguay in the departments of Maldonado, Montevideo, and Paysandú, and central eastern Argentina in the province of Entre Ríos. This species grows in dry grasslands and rocky places.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

13. Piptochaetium cucullatum Rosengurtt & Izaguirre de Arturio, Bol. Univ. Rep. Fac. Agron. Montevideo 90: 3. 1966. TYPE: Uruguay. Dpto. Salto: Termas del Arapey, próximo a la Estación, 9 Dec. 1962, *Arrillaga et al. 1512* (holotype, MVFA not seen; isotypes, BAA!, US 2951786 not seen).

Distribution. Endemic to northern Uruguay in the departments of Salto and Paysandú.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

14. Piptochaetium featherstonei (Hitchcock) Tovar, Opusc. Bot. Pharm. Complut. 4: 104. 1988. *Stipa featherstonei* Hitchc., Proc. Biol. Soc. Wash. 36: 196. 1923. TYPE: Peru. Río Blanco, 4500 m, 8–19 May 1922, *J. F. Macbride & W. Featherstone 803a* (holotype, F 517331 pro parte not seen; isotype, US not seen).

Piptochaetium juninense Tovar & Gutte, Feddes Repert. Spec. Nov. Regni Veg. 91(4): 205. 1980. TYPE: Peru. Junín: Prov. Yauli, La Oroya, Berg oberhalb Pachacayo (Puya raimondii-Vorkommen), Steiniger Abhang, Hohe, 3750 m, *Gutte 2130* (holotype, LZ not seen; isotypes, SMF not seen, USM!).

Distribution. Southwestern Peru in the departments of Ancash, Ayacucho, and Junín at elevations between 3000 and 4500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. Hitchcock (1923) mentioned that the holotype is mounted with plants of *Stipa hansmeyeri*, but, according to Soreng (pers. comm.), it is not clear if that specimen was subdivided into parts a and b by the collectors or by Hitchcock

of *P. brevicalyx* subsp. *flexuosum*). **Guanajuato:** 10 km al sur de Ibarra, Ocampo, sobre la carretera a León, *Rzedowski 50768* (MEXU). **Hidalgo:** 8 km al noreste de Pachuca, sobre la carretera a Real del Monte, *Rzedowski 35863* (MEXU, XAL); Cerro Ventoso, above Pachuca, *Pringle 7606* (MEXU); in oak woods near Real del Monte, *Rose et al. 8680* (US); Pachuca, *Hitchcock 6733* (US). **México:** rocky roadcut, 27 mi. S of San Juan del Río, *Gould 9211* (US). **San Luis Potosí:** Cerro La Bolsa, W de Cerrito de Dolores, Mun. Villa de Arriaga, *Banda et al. 132* (CAS, MO); near Cerro Prieto, *Sohns 1535* (US). **Tlaxcala:** between San Cristóbal and Calpulalpan, *Sohns 553* (MEXU, US).

Piptochaetium brevicalyx is similar to *P. hirtum*: both species share the globose floret shape, the absence of epidermal appendages on the lemma, and generally few hairs on the callus. They can be recognized because *P. hirtum* presents conspicuous longitudinal striae on the dull lemma surface, 1 or 2 rows of hooks or prickles in the crown, and both glumes 5.5–6 mm, longer than the floret.

Barkworth (1988) recognized *Piptochaetium brevicalyx* subsp. *flexuosum* based on the relatively long and widespread branches of the inflorescences. Although there are specimens with dense or extended panicles, the difference between the length of the branches is slight, and, within the studied material, there are specimens with both types of inflorescences, such as *Banda et al. 132*.

9. Piptochaetium burkartianum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 291. 1944. TYPE: Argentina. Corrientes: San Martín, La Cruz, Nov. 1936, *Parodi 12329 1/2* (holotype, BAA!).

Distribution. Endemic to Argentina; only found in the eastern province of Corrientes, at the type locality.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

10. Piptochaetium cabrerae Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 243. 1944. TYPE: Argentina. Buenos Aires: Puan, Villa Iris, 7 Nov. 1940, *Parodi 13771* (holotype, BAA!).

Distribution. Endemic to Argentina; only collected in the southwestern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

11. Piptochaetium calvescens Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 278. 1944. TYPE: Argentina. Prov. Buenos Aires: Sierra Curumalán, 600 m s.m., 10 Nov. 1932, *Parodi 10343* (holotype, BAA!).

Distribution. Central and eastern Argentina in the province of Buenos Aires, and southern Uruguay in the department of Montevideo.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

12. Piptochaetium confusum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 246. 1944. TYPE: Argentina. Entre Ríos: Concordia, 3 Nov. 1921, *Parodi 3950* (holotype, BAA!).

Distribution and ecology. Uruguay in the departments of Maldonado, Montevideo, and Paysandú, and central eastern Argentina in the province of Entre Ríos. This species grows in dry grasslands and rocky places.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

13. Piptochaetium cucullatum Rosengurtt & Izaguirre de Arturio, Bol. Univ. Rep. Fac. Agron. Montevideo 90: 3. 1966. TYPE: Uruguay. Dpto. Salto: Termas del Arapey, próximo a la Estación, 9 Dec. 1962, *Arrillaga et al. 1512* (holotype, MVFA not seen; isotypes, BAA!, US 2951786 not seen).

Distribution. Endemic to northern Uruguay in the departments of Salto and Paysandú.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

14. Piptochaetium featherstonei (Hitchcock) Tovar, Opusc. Bot. Pharm. Complut. 4: 104. 1988. *Stipa featherstonei* Hitchc., Proc. Biol. Soc. Wash. 36: 196. 1923. TYPE: Peru. Río Blanco, 4500 m, 8–19 May 1922, *J. F. Macbride & W. Featherstone 803a* (holotype, F 517331 pro parte not seen; isotype, US not seen).

Piptochaetium juninense Tovar & Gutte, Feddes Repert. Spec. Nov. Regni Veg. 91(4): 205. 1980. TYPE: Peru. Junín: Prov. Yauli, La Oroya, Berg oberhalb Pachacayo (Puya raimondii-Vorkommen), Steiniger Abhang, Hohe, 3750 m, *Gutte 2130* (holotype, LZ not seen; isotypes, SMF not seen, USM!).

Distribution. Southwestern Peru in the departments of Ancash, Ayacucho, and Junín at elevations between 3000 and 4500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. Hitchcock (1923) mentioned that the holotype is mounted with plants of *Stipa hansmeyeri*, but, according to Soreng (pers. comm.), it is not clear if that specimen was subdivided into parts a and b by the collectors or by Hitchcock himself; the US isotype has only *Stipa featherstonei* on it.

15. Piptochaetium fimbriatum (Kunth) Hitchcock, J. Wash. Acad. Sci. 23(10): 453. 1933. *Stipa fimbriata* Kunth, Nov. Gen. Sp. 1: 126. 1816. *Oryzopsis fimbriata* (Kunth) Hemsl., Biol. Cent.-Amer., Bot. 3: 538. 1885. TYPE: Mexico. Guanaxuato, Billalpando, *Humboldt & Bonpland s.n.*, Herb. HBK 4224 (holotype, P not seen; isotype, BAA!). Figures 2B, 5G.

Piptochaetium fimbriatum (Kunth) Hitchc. var. *confine* I. M. Johnst., J. Arnold Arbor. 24: 396. 1943. TYPE: Mexico. Coahuila: Sierra del Pino, La Noria, *Johnston & Mueller 486* (holotype, GH not seen; isotype, LL not seen).

Plants perennial. *Culms* 35–80 cm tall, glabrous, sometimes pubescent below the nodes; nodes 2–3, slightly compressed or enlarged, reddish, glabrous; internodes 6–11 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, (3–)5–8 cm long, glabrous. *Ligules* 1.5–2 mm long, acute, glabrous. *Leaf blades* linear, convolute or flat, 6–26 cm long, 0.9–1.1 mm wide, adaxial side conspicuously striate, glabrous on both faces, margins scabrous. *Peduncles* terete, 12–28 cm long, longitudinally striate, glabrous. *Inflorescences* 14–20 cm long, many-flowered (20 to 60 spikelets), with branches loosely disposed; pedicels flattened, 4–12 mm long, hispid. *Spikelets* fusiform to slightly obovoid, 3.5–5 mm long, 1 mm diam. *Glumes* subequal, longer than the floret, 4–6 mm long, shortly acuminate, 5- or 7-nerved. *Floret* fusiform, slightly obovoid and gibbous, 3.5–5 mm long, 1.2–1.8 mm diam. *Lemma* contracted below the crown, 3.5–5 mm long, smooth, shiny, with deciduous macrohairs, densely disposed; crown contracted at the base of the awn, inconspicuous, straight, not revolute, ca. 0.8 mm diam., without epidermal appendages; callus 0.2–0.5 mm long, blunt, obliquely truncate, hairy, the upper macrohairs reaching ⅕ the length of the floret; awn bigeniculate, 10–20 mm long, persistent, hispid to scabrous. *Palea* 3.5–3.6 mm long. *Lodicules* 2, ca. 1 mm long, subacute. *Caryopsis* fusiform, 2.5 mm long, 0.6 mm diam.; hilum linear; embryo 1/5 the length of the caryopsis.

Chromosome numbers. $2n = 44$ (Brown, 1951); $n = 21$ (Reeder, 1968); $2n = 44$ (Valencia & Costas, 1968).

Distribution. Widespread in the southern and southeastern United States and Mexico, at elevations between 1900 and 2500 m. This species has also been cited for Guatemala, in the department of Huehuetenango (Swallen, 1955; Beetle, 1977).

Additional specimens examined. U.S.A. **Arizona:** Santa Cruz Co., Canelo Hills, along road 1.5 mi. N of Canelo Pass, *Toolin & McHargue 2222* (MO); Patagonia Mts., *Kearney & Peebles 10114* (US); Cochise Co., Cave Creek Chiricahua Mountains, *Peterson & Annable 4010* (MO, US). **New Mexico:** Grant Co., Bear Mt., near Silver City, *Metcalfe 746* (US); San Miguel Co., 8.5 mi. S of Rte. 104, 15 mi. E of Las Vegas, *Hill 14632* (MO); Santa Rita Mt., Grant Co., *Metcalfe 1471* (MO, US). **Texas:** J. Davis Co., 6.8 mi. on road to "Davis Mt. Resort" (Tomahawk trail) from State Hwy. 166, 1770 m, *Brant et al. 2239* (MO); Brewster Co., rocky slope near summit of Mt. Emory, Chisos Mts., *Correll 13699* (US); Chisos Mountains, Brewster Co., 1 mi. SW of Boot Spring, 2120 m, *Moore & Steyermark 3172* (MO, US). MEXICO. **Baja California Sur:** granitic slopes surrounding long interior valley (La Laguna), S of Pico La Aguja on the Sierra La Laguna, *Breedlove & Axelrod 43293* (MO). **Chiapas:** Teopisca, Belém, 8 km NW of Teopisca along hwy. to San Cristóbal de las Casas, *Davidse et al. 29775* (MEXU). **Chihuahua:** foothills of Sierra Madre, *Pringle 3035* (MEXU); Miñacam, *Hitchcock 7741* (US). **Coahuila:** Buenavista, Saltillo, Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Madrigal A. s.n.* (XAL); Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Serrato Sánchez s.n.* (MEXU 309021). **Distrito Federal:** Cima de Toluca, *Lyonnet 48* (MO). **Durango:** on top of rugged volcanic plateau 5.3 km W of (Ejido) Los Mimbres turnoff al km 54.2 WSW of Durango and ca. halfway to El Salto, *Iltis et al. 213* (XAL). **Guanajuato:** ca. 8 km W of San Felipe, *Sohns 424* (MO, US). **Hidalgo:** open pine woods near Ocotillos between Comanche and Huasca, ca. 2200 m, *Moore & Wood Jr. 4164* (US). **Jalisco:** Mezquitic, 8 km SE del Rancho El Mortero, *Rzedowski 17704* (US). **México:** Tezcoco, lado sur de la Cañada de Aguas, 13.5 km al SE de Tezcoco, 11 km al ESE de Coatlinchán, *Koch 77110* (MEXU); roadside, old hwy. 190 between turnoff to Chalco (Hwy. 115), Santa Bárbara ca. 30 m above Azotla, *Mick & Roe 287* (XAL). **Michoacán:** 0.6 mi. E of Poblado Constitution, *Kral 25586* (MO); ca. 20 mi. W of Morelia, *Sohns 782* (US). **Nuevo León:** 28.6 mi. N of La Ascencion on Mex 60, *Brunken & Perino 234* (MO). **Oaxaca:** 7 km N de Amatlán, Nochixtlán, *Mendoza & Mérica 2640* (MO). **Puebla:** Tepeyahualco, *Calzada et al. 4645* (XAL); vicinity of San Luis Tultilanapa, *Purpus 3589* (US). **San Luis Potosí:** Cerro La Laderona, 2.5 km S de La Amapola, Escalerillas, *Zavala Ch. 862* (XAL); in canyons in the Sierra de San Miguelito, ca. 2 km W of Terrero, 1850–2200 m, 8 Sep. 1954, *Sohns 1147* (US). **Sonora:** Sierra de los Ajos, Rancho de los Ajos, Cañón de Evans, *Felger et al. 92-794* (MO). **Tamaulipas:** Marcella, *Stanford et al. 2604* (MO). **Tlaxcala:** between San Cristóbal and Capulalpan in open, lightly wooded areas, *Sohns 581* (MEXU); Contadero, *Pringle 8595* (MEXU). **Zacatecas:** 9.5 mi. W of Sombrerete, *Taylor & Taylor 6254* (US).

The epidermal surfaces of the lemma in *Piptochaetium fimbriatum* and *P. pringlei* are similar, as both species present smooth and shiny floret surfaces with the macrohairs deciduous. However, *P. pringlei* differs in having bigger florets, from 7 to 10 mm long, and a subacute callus.

himself; the US isotype has only *Stipa featherstonei* on it.

15. Piptochaetium fimbriatum (Kunth) Hitchcock, J. Wash. Acad. Sci. 23(10): 453. 1933. *Stipa fimbriata* Kunth, Nov. Gen. Sp. 1: 126. 1816. *Oryzopsis fimbriata* (Kunth) Hemsl., Biol. Cent.-Amer., Bot. 3: 538. 1885. TYPE: Mexico. Guanaxuato, Billalpando, *Humboldt & Bonpland s.n.*, Herb. HBK 4224 (holotype, P not seen; isotype, BAA!). Figures 2B, 5G.

Piptochaetium fimbriatum (Kunth) Hitchc. var. *confine* I. M. Johnst., J. Arnold Arbor. 24: 396. 1943. TYPE: Mexico. Coahuila: Sierra del Pino, La Noria, *Johnston & Mueller 486* (holotype, GH not seen; isotype, LL not seen).

Plants perennial. *Culms* 35–80 cm tall, glabrous, sometimes pubescent below the nodes; nodes 2–3, slightly compressed or enlarged, reddish, glabrous; internodes 6–11 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, (3–)5–8 cm long, glabrous. *Ligules* 1.5–2 mm long, acute, glabrous. *Leaf blades* linear, convolute or flat, 6–26 cm long, 0.9–1.1 mm wide, adaxial side conspicuously striate, glabrous on both faces, margins scabrous. *Peduncles* terete, 12–28 cm long, longitudinally striate, glabrous. *Inflorescences* 14–20 cm long, many-flowered (20 to 60 spikelets), with branches loosely disposed; pedicels flattened, 4–12 mm long, hispid. *Spikelets* fusiform to slightly obovoid, 3.5–5 mm long, 1 mm diam. *Glumes* subequal, longer than the floret, 4–6 mm long, shortly acuminate, 5- or 7-nerved. *Floret* fusiform, slightly obovoid and gibbous, 3.5–5 mm long, 1.2–1.8 mm diam. *Lemma* contracted below the crown, 3.5–5 mm long, smooth, shiny, with deciduous macrohairs, densely disposed; crown contracted at the base of the awn, inconspicuous, straight, not revolute, ca. 0.8 mm diam., without epidermal appendages; callus 0.2–0.5 mm long, blunt, obliquely truncate, hairy, the upper macrohairs reaching ⅕ the length of the floret; awn bigeniculate, 10–20 mm long, persistent, hispid to scabrous. *Palea* 3.5–3.6 mm long. *Lodicules* 2, ca. 1 mm long, subacute. *Caryopsis* fusiform, 2.5 mm long, 0.6 mm diam.; hilum linear; embryo 1/5 the length of the caryopsis.

Chromosome numbers. $2n = 44$ (Brown, 1951); $n = 21$ (Reeder, 1968); $2n = 44$ (Valencia & Costas, 1968).

Distribution. Widespread in the southern and southeastern United States and Mexico, at elevations between 1900 and 2500 m. This species has also been cited for Guatemala, in the department of Huehuetenango (Swallen, 1955; Beetle, 1977).

Additional specimens examined. U.S.A. **Arizona:** Santa Cruz Co., Canelo Hills, along road 1.5 mi. N of Canelo Pass, *Toolin & McHargue 2222* (MO); Patagonia Mts., *Kearney & Peebles 10114* (US); Cochise Co., Cave Creek Chiricahua Mountains, *Peterson & Annable 4010* (MO, US). **New Mexico:** Grant Co., Bear Mt., near Silver City, *Metcalfe 746* (US); San Miguel Co., 8.5 mi. S of Rte. 104, 15 mi. E of Las Vegas, *Hill 14632* (MO); Santa Rita Mt., Grant Co., *Metcalfe 1471* (MO, US). **Texas:** J. Davis Co., 6.8 mi. on road to "Davis Mt. Resort" (Tomahawk trail) from State Hwy. 166, 1770 m, *Brant et al. 2239* (MO); Brewster Co., rocky slope near summit of Mt. Emory, Chisos Mts., *Correll 13699* (US); Chisos Mountains, Brewster Co., 1 mi. SW of Boot Spring, 2120 m, *Moore & Steyermark 3172* (MO, US). MEXICO. **Baja California Sur:** granitic slopes surrounding long interior valley (La Laguna), S of Pico La Aguja on the Sierra La Laguna, *Breedlove & Axelrod 43293* (MO). **Chiapas:** Teopisca, Belém, 8 km NW of Teopisca along hwy. to San Cristóbal de las Casas, *Davidse et al. 29775* (MEXU). **Chihuahua:** foothills of Sierra Madre, *Pringle 3035* (MEXU); Miñacam, *Hitchcock 7741* (US). **Coahuila:** Buenavista, Saltillo, Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Madrigal A. s.n.* (XAL); Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Serrato Sánchez s.n.* (MEXU 309021). **Distrito Federal:** Cima de Toluca, *Lyonnet 48* (MO). **Durango:** on top of rugged volcanic plateau 5.3 km W of (Ejido) Los Mimbres turnoff al km 54.2 WSW of Durango and ca. halfway to El Salto, *Iltis et al. 213* (XAL). **Guanajuato:** ca. 8 km W of San Felipe, *Sohns 424* (MO, US). **Hidalgo:** open pine woods near Ocotillos between Comanche and Huasca, ca. 2200 m, *Moore & Wood Jr. 4164* (US). **Jalisco:** Mezquitic, 8 km SE del Rancho El Mortero, *Rzedowski 17704* (US). **México:** Tezcoco, lado sur de la Cañada de Aguas, 13.5 km al SE de Tezcoco, 11 km al ESE de Coatlinchán, *Koch 77110* (MEXU); roadside, old hwy. 190 between turnoff to Chalco (Hwy. 115), Santa Bárbara ca. 30 m above Azotla, *Mick & Roe 287* (XAL). **Michoacán:** 0.6 mi. E of Poblado Constitution, *Kral 25586* (MO); ca. 20 mi. W of Morelia, *Sohns 782* (US). **Nuevo León:** 28.6 mi. N of La Ascencion on Mex 60, *Brunken & Perino 234* (MO). **Oaxaca:** 7 km N de Amatlán, Nochixtlán, *Mendoza & Mérica 2640* (MO). **Puebla:** Tepeyahualco, *Calzada et al. 4645* (XAL); vicinity of San Luis Tultilanapa, *Purpus 3589* (US). **San Luis Potosí:** Cerro La Laderona, 2.5 km S de La Amapola, Escalerillas, *Zavala Ch. 862* (XAL); in canyons in the Sierra de San Miguelito, ca. 2 km W of Terrero, 1850–2200 m, 8 Sep. 1954, *Sohns 1147* (US). **Sonora:** Sierra de los Ajos, Rancho de los Ajos, Cañón de Evans, *Felger et al. 92-794* (MO). **Tamaulipas:** Marcella, *Stanford et al. 2604* (MO). **Tlaxcala:** between San Cristóbal and Capulalpan in open, lightly wooded areas, *Sohns 581* (MEXU); Contadero, *Pringle 8595* (MEXU). **Zacatecas:** 9.5 mi. W of Sombrerete, *Taylor & Taylor 6254* (US).

The epidermal surfaces of the lemma in *Piptochaetium fimbriatum* and *P. pringlei* are similar, as both species present smooth and shiny floret surfaces with the macrohairs deciduous. However, *P. pringlei* differs in having bigger florets, from 7 to 10 mm long, and a subacute callus.

16. Piptochaetium hackelii (Arechavaleta) Parodi, Revista Fac. Agron. Veterin. 7(1): 162. 1930. *Stipa hackelii* Arechav., Anales Mus. Nac. Hist. Nat. Buenos Aires 4: 179. 1895. *Oryzopsis hackelii* (Arechav.) Speg., Anales Mus. Nac. Montevideo 4(2): 10. 1901. *Piptochaetium hackelii* (Arechav.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Cerro de Montevideo, cerca de la cumbre, *Arechavaleta 39 a* (holotype, not located; isotype, LPS 2486!, US not seen).

Stipa tandilensis Kuntze, Rev. Gen. Pl. 3(2): 373. 1898. TYPE: Argentina. Buenos Aires: Tandil, Nov. 1892, *Otto Kuntze s.n.* (holotype, NY!).

Distribution. This species grows in the grasslands of Uruguay in the departments of Lavalleja, Maldonado, and Río Negro, as well as in central Argentina in the provinces of Buenos Aires and La Pampa.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. The holotype of *Stipa hackelii* Arechav. could not be located. According to Alonso Paz (pers. comm.), Arechavaleta did not choose types, so in many cases a lectotype must be designated.

17. Piptochaetium hirtum Philippi, Anales Univ. Chile 43: 559. 1873. TYPE: Chile. Cerro de Renca, Dec. 1864, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45078!; isolectotypes, K!, SGO 57422!).

Piptochaetium brevifolium Phil., Anales Univ. Chile 93: 733. 1896. TYPE: Chile. Cerro de Renca, 11 Nov. 1877, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45077!; isolectotypes, SGO 45078!, SGO 57421!).

Distribution. Known from Cerro de Renca in Chile and San Martín de los Andes in the province of Neuquen in Argentina (Parodi, 1961).

For a description and illustrations, see Cialdella and Arriaga (1998).

18. Piptochaetium indutum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 258. 1944. TYPE: Argentina. Salta: Rosario de Lerma, Puerta Tastil, 2700 m, *Venturi 8414* (holotype, US not seen; isotype, BAA!).

Distribution. Originally known from northern Argentina from the provinces of Salta and Jujuy, distributed in Bolivia in the departments of La Paz and Potosí, central western Peru in the departments of Ancash, La Libertad, and Lima, between 2500 and 4500 m; it is also cited from Ecuador in the province of Azuay (Jørgensen & León-Yánez, 1999).

Additional specimens examined. PERU. **Ancash:** Recuay Prov., Huascaran Nat. Park, Río Pachacoto, *Smith & Torres 11794 A* (MO); Yungas Prov., Huascarán National Park, Llanganuco Sector, *Smith 10488* (MO); Recuay Prov., Quebrada Huanca, *Smith & Buddensiek 10964* (MO). **La Libertad:** Sánchez Carrion Prov., Trujillo–Huamachuco road, 20 km W of Huamachuco, *Smith & Vásquez M. 3327* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

19. Piptochaetium jubatum Henrard, Recueil Trav. Bot. Néerl. 36: 537. 1939. TYPE: Uruguay. Canelones: Río Santa Lucía, Paso Cuello, *Gallinal et al. 2198* (holotype, Herb. Lugd. Bat. n. 938,280–383, L!; isotypes, US 1723425 not seen, BAA!).

Distribution. Known only from the department of Canelones in Uruguay.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

20. Piptochaetium lasianthum Grisebach, Symb. Fl. Argent.: 297. 1879. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, Quinta del Colegio, en praderas, *Lorentz s.n., Flora Entrerriana n. 1157* (holotype, not located; isotype, CORD!).

Piptochaetium erianthum Balansa, Bull. Soc. Bot. France 32: 244. 1885. TYPE: Uruguay. Cerro de Montevideo, 1874, *Balansa 9* (holotype, not located).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, central and southern Uruguay in the departments of Flores, Lavalleja, and Montevideo, and widespread in central eastern Argentina in the provinces of Buenos Aires, Córdoba, Corrientes, Entre Ríos, Misiones, and Santa Fe.

Additional specimen examined. ARGENTINA. **Misiones:** Candelaria, Villa Venecia, *Renvoize et al. 3025* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

21. Piptochaetium lejopodum (Spegazzini) Henrard, Recueil Trav. Bot. Néerl. 36: 536. 1939. *Oryzopsis lejopoda* Speg., Anales Mus. Nac. Montevideo 4(2): 19. 1901. TYPE: Argentina. Buenos Aires: Sierra de la Ventana, Valle de las Vertientes, Nov. 1895, *C. L. Spegazzini s.n.* (holotype, LPS 12666!).

Distribution. Southern Uruguay in the depart-

16. Piptochaetium hackelii (Arechavaleta) Parodi, Revista Fac. Agron. Veterin. 7(1): 162. 1930. *Stipa hackelii* Arechav., Anales Mus. Nac. Hist. Nat. Buenos Aires 4: 179. 1895. *Oryzopsis hackelii* (Arechav.) Speg., Anales Mus. Nac. Montevideo 4(2): 10. 1901. *Piptochaetium hackelii* (Arechav.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Cerro de Montevideo, cerca de la cumbre, *Arechavaleta 39 a* (holotype, not located; isotype, LPS 2486!, US not seen).

Stipa tandilensis Kuntze, Rev. Gen. Pl. 3(2): 373. 1898. TYPE: Argentina. Buenos Aires: Tandil, Nov. 1892, *Otto Kuntze s.n.* (holotype, NY!).

Distribution. This species grows in the grasslands of Uruguay in the departments of Lavalleja, Maldonado, and Río Negro, as well as in central Argentina in the provinces of Buenos Aires and La Pampa.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. The holotype of *Stipa hackelii* Arechav. could not be located. According to Alonso Paz (pers. comm.), Arechavaleta did not choose types, so in many cases a lectotype must be designated.

17. Piptochaetium hirtum Philippi, Anales Univ. Chile 43: 559. 1873. TYPE: Chile. Cerro de Renca, Dec. 1864, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45078!; isolectotypes, K!, SGO 57422!).

Piptochaetium brevifolium Phil., Anales Univ. Chile 93: 733. 1896. TYPE: Chile. Cerro de Renca, 11 Nov. 1877, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45077!; isolectotypes, SGO 45078!, SGO 57421!).

Distribution. Known from Cerro de Renca in Chile and San Martín de los Andes in the province of Neuquen in Argentina (Parodi, 1961).

For a description and illustrations, see Cialdella and Arriaga (1998).

18. Piptochaetium indutum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 258. 1944. TYPE: Argentina. Salta: Rosario de Lerma, Puerta Tastil, 2700 m, *Venturi 8414* (holotype, US not seen; isotype, BAA!).

Distribution. Originally known from northern Argentina from the provinces of Salta and Jujuy, distributed in Bolivia in the departments of La Paz and Potosí, central western Peru in the departments of Ancash, La Libertad, and Lima, between 2500 and 4500 m; it is also cited from Ecuador in the province of Azuay (Jørgensen & León-Yánez, 1999).

Additional specimens examined. PERU. **Ancash:** Recuay Prov., Huascaran Nat. Park, Río Pachacoto, *Smith & Torres 11794 A* (MO); Yungas Prov., Huascarán National Park, Llanganuco Sector, *Smith 10488* (MO); Recuay Prov., Quebrada Huanca, *Smith & Buddensiek 10964* (MO). **La Libertad:** Sánchez Carrion Prov., Trujillo–Huamachuco road, 20 km W of Huamachuco, *Smith & Vásquez M. 3327* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

19. Piptochaetium jubatum Henrard, Recueil Trav. Bot. Néerl. 36: 537. 1939. TYPE: Uruguay. Canelones: Río Santa Lucía, Paso Cuello, *Gallinal et al. 2198* (holotype, Herb. Lugd. Bat. n. 938,280–383, L!; isotypes, US 1723425 not seen, BAA!).

Distribution. Known only from the department of Canelones in Uruguay.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

20. Piptochaetium lasianthum Grisebach, Symb. Fl. Argent.: 297. 1879. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, Quinta del Colegio, en praderas, *Lorentz s.n.*, *Flora Entrerriana n. 1157* (holotype, not located; isotype, CORD!).

Piptochaetium erianthum Balansa, Bull. Soc. Bot. France 32: 244. 1885. TYPE: Uruguay. Cerro de Montevideo, 1874, *Balansa 9* (holotype, not located).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, central and southern Uruguay in the departments of Flores, Lavalleja, and Montevideo, and widespread in central eastern Argentina in the provinces of Buenos Aires, Córdoba, Corrientes, Entre Ríos, Misiones, and Santa Fe.

Additional specimen examined. ARGENTINA. **Misiones:** Candelaria, Villa Venecia, *Renvoize et al. 3025* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

21. Piptochaetium lejopodum (Spegazzini) Henrard, Recueil Trav. Bot. Néerl. 36: 536. 1939. *Oryzopsis lejopoda* Speg., Anales Mus. Nac. Montevideo 4(2): 19. 1901. TYPE: Argentina. Buenos Aires: Sierra de la Ventana, Valle de las Vertientes, Nov. 1895, *C. L. Spegazzini s.n.* (holotype, LPS 12666!).

Distribution. Southern Uruguay in the departments of Lavalleja and Maldonado, and central eastern Argentina in southern Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

22. Piptochaetium medium (Spegazzini) Torres, Bol. Soc. Argent. Bot. 11(4): 251. 1969. *Oryzopsis bicolor* (Vahl) Speg. var. *media* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini s.n.* (lectotype, designated by Torres (1969), LPS 12517!).

Distribution. Southern Brazil in the state of Rio Grande do Sul, southern Uruguay in the department of Florida, and eastern Argentina, widespread in the provinces of Buenos Aires, Córdoba, Entre Ríos, La Pampa, Misiones, and Santa Fe.

Additional specimens examined. BRAZIL. **Rio Grande do Sul:** Esmeralda, 29 Nov. 1988, *M. Sallés 141, 142* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

23. Piptochaetium montevidense (Sprengel) Parodi, Revista Fac. Agron. Veterin. 7(1): 163. 1930. *Caryochloa montevidensis* Spreng., Syst. Veg. 4(2): 30. 1827. *Oryzopsis montevidensis* (Spreng.) Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 116. 1917. *Oryzopsis montevidensis* (Spreng.) Speg., Revista Argent. Bot. 1(1): 10. 1925, comb. superfl. *Oryzopsis montevidensis* (Spreng.) Speg. f. *typica* Speg., Revista Argent. Bot. 1(1): 11. 1925, nom. inval. *Piptochaetium montevidense* (Spreng.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Montevideo: *Sellow s.n.* (holotype, B not seen; isotype, MO!).

Urachne panicoides Trin. var. *brasiliensis* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 23. 1842. *Caryochloa montevidensis* Spreng. var. *brasiliensis* (Trin. & Rupr.) Döll ex Ekman, Ark. Bot. 13(10): 40. 1913. TYPE: "A Montevideo usque ad fines regni Paraguayani," *Sellow s.n.* (holotype, not located).

Piptochaetium tuberculatum E. Desv., in Gay, Fl. Chil. 6: 272. 1853. *Oryzopsis tuberculata* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 26. 1901. TYPE: Chile. Valdivia: *Gay s.n.* (holotype, P!).

Urachne depressa Steud., Syn. Pl. Glumac. 1: 123. 1854. TYPE: Chile. Rancagua: *Bertero 456* (holotype, P!).

Piptochaetium verrucosum Phil., Linnaea 33: 280. 1865. *Oryzopsis verruculosa* (Phil.) Speg., error for *verrucosa*, Anales Mus. Nac. Montevideo 4(2): 28. 1901. *Oryzopsis verrucosa* (Phil.) Speg., Revista Argent. Bot. 1(1): 12. 1925. TYPE: Chile. Valdivia: San Juan, *Philippi s.n.* (holotype, SGO 57334!; probable isotype, SGO 57350!).

Piptochaetium humile Phil., Anales Univ. Chile 93: 730. 1896. TYPE: Chile. Concon: médanos, *Philippi s.n.* (holotype, SGO 45087!).

Piptochaetium granulatum Phil., Anales Univ. Chile 93: 732. 1896. TYPE: Chile. Concon: *Philippi s.n.* (holotype, SGO 57333!).

Piptochaetium moelleri Phil., Anales Univ. Chile 93: 734. 1896. TYPE: Chile. Renaico, *Möller s.n.* (holotype, SGO 57332!).

Oryzopsis montevidensis (Spreng.) Speg. f. *trachycarpa* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Argentina. Misiones: Posadas, praderas de los alrededores, *Spegazzini s.n.* (holotype, LPS 13166!).

Oryzopsis montevidensis (Spreng.) Speg. f. *brasiliensis* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Brazil. Rio Grande do Sul: Uruguayana, campos secos, *Spegazzini s.n.* (holotype, LPS 13175!).

Distribution. Found in Venezuela in the state of Trujillo, and widespread in southern South America in Bolivia, departments of La Paz and Cochabamba, central Chile, IV, VI, and VIII Regions, southern Paraguay, departments of Misiones and Paraguarí, southern Brazil, states of Paraná, Rio Grande do Sul, and Santa Catarina, southern Uruguay, departments of Colonia, Lavalleja, and Maldonado, and northern and central Argentina, provinces of Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. This species, which has been considered disjunct in Mexico, northern South America, and southern South America (Thomasson, 1980), has also been cited for Peru (Brako & Zarucchi, 1993) and southern Ecuador, province of Chinchipe (Jørgensen & León-Yánez, 1999). This distribution pattern makes it probable that it also occurs in Colombia, and, together with *P. panicoides*, would confirm one of the possible migration routes proposed by Thomasson (1980).

This species is the most frequent of the genus, growing on riversides, grasslands with rocky places and modified soils, up to 3700 m elevation.

Additional specimens examined. BRAZIL. **Paraná:** Ruta BR-280, hacia Horizonte, a 1 km de ruta BR-153, *Rúgolo et al. 1611* (MO). VENEZUELA. **Trujillo:** Carache, 220 m, *Rivero & Díaz 1384* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

24. Piptochaetium napostaense (Spegazzini) Hackel, Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 103. 1904. *Oryzopsis napostaensis* Speg., Anales Mus. Nac. Montevideo 4(2): 15. 1901. *Oryzopsis napostaensis* Speg. var. *macrophylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: alrededores de Carmen de Patagones, Feb. 1898, *C. L. Spegazzini 41 a* (lectotype, designated by Parodi (1944), LPS 2483!).

ments of Lavalleja and Maldonado, and central eastern Argentina in southern Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

22. Piptochaetium medium (Spegazzini) Torres, Bol. Soc. Argent. Bot. 11(4): 251. 1969. *Oryzopsis bicolor* (Vahl) Speg. var. *media* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini s.n.* (lectotype, designated by Torres (1969), LPS 12517!).

Distribution. Southern Brazil in the state of Rio Grande do Sul, southern Uruguay in the department of Florida, and eastern Argentina, widespread in the provinces of Buenos Aires, Córdoba, Entre Ríos, La Pampa, Misiones, and Santa Fe.

Additional specimens examined. BRAZIL. **Rio Grande do Sul:** Esmeralda, 29 Nov. 1988, *M. Sallés 141, 142* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

23. Piptochaetium montevidense (Sprengel) Parodi, Revista Fac. Agron. Veterin. 7(1): 163. 1930. *Caryochloa montevidensis* Spreng., Syst. Veg. 4(2): 30. 1827. *Oryzopsis montevidensis* (Spreng.) Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 116. 1917. *Oryzopsis montevidensis* (Spreng.) Speg., Revista Argent. Bot. 1(1): 10. 1925, comb. superfl. *Oryzopsis montevidensis* (Spreng.) Speg. f. *typica* Speg., Revista Argent. Bot. 1(1): 11. 1925, nom. inval. *Piptochaetium montevidense* (Spreng.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Montevideo: *Sellow s.n.* (holotype, B not seen; isotype, MO!).

Urachne panicoides Trin. var. *brasiliensis* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 23. 1842. *Caryochloa montevidensis* Spreng. var. *brasiliensis* (Trin. & Rupr.) Döll ex Ekman, Ark. Bot. 13(10): 40. 1913. TYPE: "A Montevideo usque ad fines regni Paraguayani," *Sellow s.n.* (holotype, not located).

Piptochaetium tuberculatum E. Desv., in Gay, Fl. Chil. 6: 272. 1853. *Oryzopsis tuberculata* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 26. 1901. TYPE: Chile. Valdivia: *Gay s.n.* (holotype, P!).

Urachne depressa Steud., Syn. Pl. Glumac. 1: 123. 1854. TYPE: Chile. Rancagua: *Bertero 456* (holotype, P!).

Piptochaetium verrucosum Phil., Linnaea 33: 280. 1865. *Oryzopsis verruculosa* (Phil.) Speg., error for *verrucosa*, Anales Mus. Nac. Montevideo 4(2): 28. 1901. *Oryzopsis verrucosa* (Phil.) Speg., Revista Argent. Bot. 1(1): 12. 1925. TYPE: Chile. Valdivia: San Juan, *Philippi s.n.* (holotype, SGO 57334!; probable isotype, SGO 57350!).

Piptochaetium humile Phil., Anales Univ. Chile 93: 730. 1896. TYPE: Chile. Concon: médanos, *Philippi s.n.* (holotype, SGO 45087!).

Piptochaetium granulatum Phil., Anales Univ. Chile 93: 732. 1896. TYPE: Chile. Concon: *Philippi s.n.* (holotype, SGO 57333!).

Piptochaetium moelleri Phil., Anales Univ. Chile 93: 734. 1896. TYPE: Chile. Renaico, *Möller s.n.* (holotype, SGO 57332!).

Oryzopsis montevidensis (Spreng.) Speg. f. *trachycarpa* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Argentina. Misiones: Posadas, praderas de los alrededores, *Spegazzini s.n.* (holotype, LPS 13166!).

Oryzopsis montevidensis (Spreng.) Speg. f. *brasiliensis* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Brazil. Rio Grande do Sul: Uruguayana, campos secos, *Spegazzini s.n.* (holotype, LPS 13175!).

Distribution. Found in Venezuela in the state of Trujillo, and widespread in southern South America in Bolivia, departments of La Paz and Cochabamba, central Chile, IV, VI, and VIII Regions, southern Paraguay, departments of Misiones and Paraguarí, southern Brazil, states of Paraná, Rio Grande do Sul, and Santa Catarina, southern Uruguay, departments of Colonia, Lavalleja, and Maldonado, and northern and central Argentina, provinces of Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. This species, which has been considered disjunct in Mexico, northern South America, and southern South America (Thomasson, 1980), has also been cited for Peru (Brako & Zarucchi, 1993) and southern Ecuador, province of Chinchipe (Jørgensen & León-Yánez, 1999). This distribution pattern makes it probable that it also occurs in Colombia, and, together with *P. panicoides*, would confirm one of the possible migration routes proposed by Thomasson (1980).

This species is the most frequent of the genus, growing on riversides, grasslands with rocky places and modified soils, up to 3700 m elevation.

Additional specimens examined. BRAZIL. **Paraná:** Ruta BR-280, hacia Horizonte, a 1 km de ruta BR-153, *Rúgolo et al. 1611* (MO). VENEZUELA. **Trujillo:** Carache, 220 m, *Rivero & Díaz 1384* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

24. Piptochaetium napostaense (Spegazzini) Hackel, Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 103. 1904. *Oryzopsis napostaensis* Speg., Anales Mus. Nac. Montevideo 4(2): 15. 1901. *Oryzopsis napostaensis* Speg. var. *macrophylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: alrededores de Carmen de Patagones, Feb. 1898, *C. L. Spegazzini 41 a* (lectotype, designated by Parodi (1944), LPS 2483!).

Oryzopsis napostaensis Speg. var. *brachyphylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini 41 b* (holotype, LPS 2469!).

Stipa capillifolia Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 95. 1904. TYPE: Argentina. Córdoba: Dep. Río I, pedanía, Villamonte, Ea. San Teodoro, *Stuckert 13803* (syntype, W not seen; isosyntypes, CORD!, LPS!), *Stuckert 14082* (syntype, not located).

Stipa hypogona Hack., Anales Mus. Nac. Buenos Aires 21: 73. 1911. TYPE: Argentina. Buenos Aires: Estación Tornquist, F.C.S., *M. Estrada s.n.*, Herb. *Stuckert 17397* (holotype, W not seen; isotype, US 3168626 not seen).

Distribution. Endemic to central Argentina in the provinces of Buenos Aires, Catamarca, Córdoba, La Pampa, Mendoza, Río Negro, and San Luis, up to 1900–2000 m elevation. This species grows in dry and arid grasslands and is a frequent species of the "caldenal," an open wild forest of "calden tree" (*Prosopis caldenia* Burkart), in the "Espinal" biogeographic province.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

25. Piptochaetium palustre Mujica-Sallés & Longhi-Wagner, Candollea 48: 15. 1993. TYPE: Brazil. Santa Catarina: Urupema, junto a la Estación Retransmisora del Morro de Campo Novo, 1680 m s.m., 25 Nov. 1984, *J. F. M. Valls et al. 8083* (holotype, ICN!; isotype, CEN!).

Distribution. Known only from southern Brazil at the type locality.

For a description and illustrations, see Cialdella and Arriaga (1998).

26. Piptochaetium panicoides (Lamarck) E. Desvaux, in Gay, Fl. Chil. 6: 270. 1853. *Stipa panicoides* Lam., Illustr. Genr. 1: 158. 1791. *Oryzopsis panicoides* (Lam.) Speg., Anales Mus. Nac. Montevideo 4(2): 31. 1901. TYPE: Uruguay. Montevideo: without locality, 1767, *Commerson s.n.* (isotypes, P!, MPU not seen, US not seen).

Oryzopsis setacea A. Rich., Dict. Hist. Nat. 12: 445. 1827. TYPE: Uruguay. Montevideo: *Commerson s.n.* (holotype, probably P not seen).

Piptochaetium setifolium J. Presl, Reliq. Haenk. 1: 222. 1830. *Stipa setifolia* (J. Presl) Kunth, Enum. Pl. 1: 182. 1833. *Urachne simplex* Trin. & Rupr. var. *peruviana* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 23. 1842. *Oryzopsis setifolia* (J. Presl) Henrard, Meded. Rijks-Herb. 40: 57. 1921. TYPE: Peru. Sin localidad, *T. Haenke s.n.* (holotype, PR!).

Oryzopsis lejocarpa Speg., Anales Mus. Nac. Montevideo 4(2): 33. 1901. *Piptochaetium leiocarpum* (Speg.) Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, not located; isotype, LPS!).

Piptochaetium subnudum Phil., Anales Univ. Chile 93: 731. 1896. TYPE: Chile. Río Itata, *Philippi s.n.* (holotype, SGO not seen; isotypes, SGO 57374!, US not seen).

Piptochaetium leiocarpum (Speg.) Hack. f. *subpapillosa* Hack. ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. *Piptochaetium panicoides* (Lam.) E. Desv. f. *subpapillosum* (Hack. ex Stuck.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 302. 1944. *Piptochaetium panicoides* (Lam.) E. Desv. var. *subpapillosum* (Hack. ex Stuck.) Petetin, in Correa, Fl. Patagónica, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 8(3): 339. 1978. TYPE: Argentina. Tucumán: without locality, *Lillo 4314* (holotype, not located; isotype, Herb. Arg. Stuckert 15418, CORD!).

Stipa lineolata Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 205. 1921. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, B not seen).

Oryzopsis lejocarpa Speg. var. *major* Speg., Revista Argent. Bot. 1(1): 10. 1925. TYPE: Argentina. Jujuy: Sierra de Santa Bárbara, Sta. Cornelia, *Spegazzini 2490* (holotype, LPS 12641!).

Distribution. This species has a disjunct distribution within South America: an Andean area, including mountain regions of Venezuela, Colombia, and Peru (Brako & Zarucchi, 1993), widespread in Ecuador (Jørgensen & León-Yánez, 1999), Bolivia, Chile, and Argentina, in the provinces of Córdoba, Jujuy, Salta, and Tucumán, and a coastal zone limited to sandy soils of southern Brazil, Uruguay, and Argentina, in the provinces of Buenos Aires and Entre Ríos.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

27. Piptochaetium pilosum (Sánchez Vega) Cialdella & Giussani, stat. nov. Basionym: *Piptochaetium tovarii* Sánchez Vega subsp. *pilosa* Sánchez Vega, Arnaldoa 1(1): 29. 1991. TYPE: Peru. Cajamarca: entre Llacanora y Namora, 2750 m, *Sánchez Vega et al. 2459* (holotype, CPUN!; isotypes, MO!, USM!).

The florets of this species have lemmas with prickles, hooks, and macrohairs all over the surface, and a callus that is densely pubescent. These characters clearly distinguish *Piptochaetium pilosum* from *P. tovarii*, with florets without any epidermal appendage on the lemma and callus. These differences, together with the results of the cladistic analysis, make it reasonable to raise *Piptochaetium tovarii* subsp. *pilosa* to the rank of species.

Distribution. Peru in the departments of Cajamarca and Junín.

Oryzopsis napostaensis Speg. var. *brachyphylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini 41 b* (holotype, LPS 2469!).

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Distribution. Endemic to central Argentina in the provinces of Buenos Aires, Catamarca, Córdoba, La Pampa, Mendoza, Río Negro, and San Luis, up to 1900–2000 m elevation. This species grows in dry and arid grasslands and is a frequent species of the "caldenal," an open wild forest of "calden tree" (*Prosopis caldenia* Burkart), in the "Espinal" biogeographic province.

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Distribution. Known only from southern Brazil at the type locality.

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Oryzopsis lejocarpa Speg., Anales Mus. Nac. Montevideo 4(2): 33. 1901. *Piptochaetium leiocarpum* (Speg.) Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, not located; isotype, LPS!).

Piptochaetium subnudum Phil., Anales Univ. Chile 93: 731. 1896. TYPE: Chile. Río Itata, *Philippi s.n.* (holotype, SGO not seen; isotypes, SGO 57374!, US not seen).

Piptochaetium leiocarpum (Speg.) Hack. f. *subpapillosa* Hack. ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. *Piptochaetium panicoides* (Lam.) E. Desv. f. *subpapillosum* (Hack. ex Stuck.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 302. 1944. *Piptochaetium panicoides* (Lam.) E. Desv. var. *subpapillosum* (Hack. ex Stuck.) Petetin, in Correa, Fl. Patagónica, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 8(3): 339. 1978. TYPE: Argentina. Tucumán: without locality, *Lillo 4314* (holotype, not located; isotype, Herb. Arg. Stuckert 15418, CORD!).

Stipa lineolata Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 205. 1921. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, B not seen).

Oryzopsis lejocarpa Speg. var. *major* Speg., Revista Argent. Bot. 1(1): 10. 1925. TYPE: Argentina. Jujuy: Sierra de Santa Bárbara, Sta. Cornelia, *Spegazzini 2490* (holotype, LPS 12641!).

Distribution. This species has a disjunct distribution within South America: an Andean area, including mountain regions of Venezuela, Colombia, and Peru (Brako & Zarucchi, 1993), widespread in Ecuador (Jørgensen & León-Yánez, 1999), Bolivia, Chile, and Argentina, in the provinces of Córdoba, Jujuy, Salta, and Tucumán, and a coastal zone limited to sandy soils of southern Brazil, Uruguay, and Argentina, in the provinces of Buenos Aires and Entre Ríos.

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Distribution. Peru in the departments of Cajamarca and Junín.

For a description and illustrations, see Cialdella and Arriaga (1998).

28. Piptochaetium pringlei (Beal) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 230. 1944. *Oryzopsis pringlei* Beal, Bot. Gaz. 15: 112. 1890. *Stipa pringlei* (Beal) Scribn., in Vasey, Contr. U.S. Natl. Herb. 3(1): 54. 1892. TYPE: Mexico. Chihuahua: dry ledges, Sierra Madre, 5 Nov. 1887, 8500 ft., *Pringle 1410* (holotype, US!; isotype, MO!). Figure 5D.

Plants perennial. *Culms* 0.5–1 m tall, terete, glabrous, pubescent below the nodes; nodes 2–3, reddish, compressed or enlarged, glabrous or slightly pubescent; internodes 7–20 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 6–18 cm long, scabrous, hispid to the base. *Ligules* 1–2.5 mm long, blunt or subacute, margins entire, hispid at the abaxial side. *Leaf blades* linear, flat, 10–30 cm long, 1–3 mm wide, glabrous, scabrous on the nerves and margins. *Peduncles* terete, slightly flattened, 30–50 cm long, longitudinally striate, hispid. *Inflorescences* 15–16 cm long, few-flowered (10 to 25 spikelets), with branches loosely disposed; pedicels flattened, up to 1 mm long, hispid. *Spikelets* fusiform, 9–12 mm long, 1.2–1.9 mm diam. *Glumes* subequal, longer than the floret, 9–12 mm long, acuminate, glabrous; lower glume 5- or 7-nerved; upper glume 7-nerved. *Floret* terete-fusiform, 7–10 mm long, 1–1.5(–1.9) mm diam. *Lemma* contracted below the crown, 7–10 mm long, smooth, shiny, with yellowish macrohairs, deciduous, and few prickles toward the crown; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.4–0.8 mm diam., with rows of long macrohairs 0.8–1 mm long and prickles; callus 0.8–1 mm long, subacute, obliquely truncate, hairy, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 1–2 (–3.5) cm long, persistent, hispid, scabrous toward the apex. *Palea* 6–7 mm long. Lodicules 2, ca. 1 mm long, acute. *Caryopsis* not seen.

Chromosome numbers. $2n = 42$ (Myers, 1947, as *Stipa pringlei* (Beal) Scribn.); $n = 21$ (Reeder, 1977, as *Stipa pringlei* (Beal) Scribn.).

Distribution. Southwestern United States and northern Mexico, up to 2000–2500 m elevation.

Additional specimens examined. U.S.A. **Arizona:** Cochise Co., 6 mi. up Carr Canyon, Huachuca Mountains, *Gould et al. 2456* (BAA, US); Williams, *Hitchcock 1903* (US); Mt. Lemmon, Santa Catalina Mts., near Tucson, *Soderstrom 141* (US). **California:** Santa Rita, *Silveus 3470* (TEX). **New Mexico:** Ranger Station, Queen, *Hitchcock 813* (BAA); Guadalupe Mountains, *Hitchcock 13553* (US). **Texas:** Black Mountains, *Tharp 4175* (TEX, US); Culberson Co., S McKittrick Canyon, top of Guadalupe Mts., *Warnock 12082* (TEX); Lincoln Co., *Hinckley & Hinckley 245* (TEX). MEXICO. **Coahuila:** Del Carmen Mts., *Marsh Jr. 629* (US). **Chihuahua:** Sierra Madre Occidental, Sierra Gazachic 35 km SW of Minaca, *Pennell 18929* (US); Sierra La Viga, 6 km E de Jame, Puerto Maravillas, *Villarreal et al. 1975* (XAL). **Sonora:** Morelos, El Rancho de Robles, *Vera Santos 1959* (MO, US); E of Cananea, Sierra de Los Ajos, *Beetle M-7856* (MO).

Piptochaetium pringlei is slightly similar to *P. fimbriatum* in that both species share the smooth surface of the lemma, only with macrohairs and few hooks near the crown. *Piptochaetium fimbriatum* differs in having a shorter floret, 3.5–5 mm long, and a blunt callus.

29. Piptochaetium ruprechtianum E. Desvaux, in Gay, Fl. Chil. 6: 274. 1853. *Oryzopsis ruprechtiana* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 12. 1901. *Stipa ruprechtiana* (E. Desv.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. TYPE: Brazil. Without locality, *Sellow s.n.* (holotype, LE-Trin not seen; isotype, US not seen; drawing of US isotype, *Herb. Parodi 4127* sheet b, BAA!).

Oryzopsis bicolor (Vahl) Speg. var. *major* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Sierra de Tandil, *Spegazzini s.n.* (holotype, LPS 12515!; isotype, BAA!).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, Uruguay in the departments of Lavalleja, Maldonado, and Soriano, and Argentina in the provinces of Misiones and Buenos Aires. This species is frequent in rocky prairies, and in Brazil it grows in savannas.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

30. Piptochaetium sagasteguii Sánchez Vega, Arnaldoa 1(1): 17. 1991. TYPE: Peru. Cajamarca: Cerro El Guitarrero, ladera occidental del valle de Cajamarca, 2800 m, 15 Jan. 1983, *I. Sánchez Vega 2914* (holotype, CPUN!; isotypes, AAU not seen, CHAPA not seen, F not seen, HAO not seen, K not seen, MO!, US 3232467 not seen, USM not seen).

Distribution. Known from Peru in the departments of Cajamarca and La Libertad at elevations between 2700 and 3500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

For a description and illustrations, see Cialdella and Arriaga (1998).

28. Piptochaetium pringlei (Beal) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 230. 1944. *Oryzopsis pringlei* Beal, Bot. Gaz. 15: 112. 1890. *Stipa pringlei* (Beal) Scribn., in Vasey, Contr. U.S. Natl. Herb. 3(1): 54. 1892. TYPE: Mexico. Chihuahua: dry ledges, Sierra Madre, 5 Nov. 1887, 8500 ft., *Pringle 1410* (holotype, US!; isotype, MO!). Figure 5D.

Plants perennial. *Culms* 0.5–1 m tall, terete, glabrous, pubescent below the nodes; nodes 2–3, reddish, compressed or enlarged, glabrous or slightly pubescent; internodes 7–20 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 6–18 cm long, scabrous, hispid to the base. *Ligules* 1–2.5 mm long, blunt or subacute, margins entire, hispid at the abaxial side. *Leaf blades* linear, flat, 10–30 cm long, 1–3 mm wide, glabrous, scabrous on the nerves and margins. *Peduncles* terete, slightly flattened, 30–50 cm long, longitudinally striate, hispid. *Inflorescences* 15–16 cm long, few-flowered (10 to 25 spikelets), with branches loosely disposed; pedicels flattened, up to 1 mm long, hispid. *Spikelets* fusiform, 9–12 mm long, 1.2–1.9 mm diam. *Glumes* subequal, longer than the floret, 9–12 mm long, acuminate, glabrous; lower glume 5- or 7-nerved; upper glume 7-nerved. *Floret* terete-fusiform, 7–10 mm long, 1–1.5(–1.9) mm diam. *Lemma* contracted below the crown, 7–10 mm long, smooth, shiny, with yellowish macrohairs, deciduous, and few prickles toward the crown; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.4–0.8 mm diam., with rows of long macrohairs 0.8–1 mm long and prickles; callus 0.8–1 mm long, subacute, obliquely truncate, hairy, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 1–2 (–3.5) cm long, persistent, hispid, scabrous toward the apex. *Palea* 6–7 mm long. Lodicules 2, ca. 1 mm long, acute. *Caryopsis* not seen.

Chromosome numbers. $2n = 42$ (Myers, 1947, as *Stipa pringlei* (Beal) Scribn.); $n = 21$ (Reeder, 1977, as *Stipa pringlei* (Beal) Scribn.).

Distribution. Southwestern United States and northern Mexico, up to 2000–2500 m elevation.

Additional specimens examined. U.S.A. **Arizona:** Cochise Co., 6 mi. up Carr Canyon, Huachuca Mountains, *Gould et al. 2456* (BAA, US); Williams, *Hitchcock 1903* (US); Mt. Lemmon, Santa Catalina Mts., near Tucson, *Soderstrom 141* (US). **California:** Santa Rita, *Silveus 3470* (TEX). **New Mexico:** Ranger Station, Queen, *Hitchcock 813* (BAA); Guadalupe Mountains, *Hitchcock 13553* (US). **Texas:** Black Mountains, *Tharp 4175* (TEX, US); Culberson Co., S McKittrick Canyon, top of Guadalupe Mts., *Warnock 12082* (TEX); Lincoln Co., *Hinckley & Hinckley 245* (TEX). MEXICO. **Coahuila:** Del Carmen Mts., *Marsh Jr. 629* (US). **Chihuahua:** Sierra Madre Occidental, Sierra Gazachic 35 km SW of Minaca, *Pennell 18929* (US); Sierra La Viga, 6 km E de Jame, Puerto Maravillas, *Villarreal et al. 1975* (XAL). **Sonora:** Morelos, El Rancho de Robles, *Vera Santos 1959* (MO, US); E of Cananea, Sierra de Los Ajos, *Beetle M-7856* (MO).

Piptochaetium pringlei is slightly similar to *P. fimbriatum* in that both species share the smooth surface of the lemma, only with macrohairs and few hooks near the crown. *Piptochaetium fimbriatum* differs in having a shorter floret, 3.5–5 mm long, and a blunt callus.

29. Piptochaetium ruprechtianum E. Desvaux, in Gay, Fl. Chil. 6: 274. 1853. *Oryzopsis ruprechtiana* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 12. 1901. *Stipa ruprechtiana* (E. Desv.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. TYPE: Brazil. Without locality, *Sellow s.n.* (holotype, LE-Trin not seen; isotype, US not seen; drawing of US isotype, *Herb. Parodi 4127* sheet b, BAA!).

Oryzopsis bicolor (Vahl) Speg. var. *major* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Sierra de Tandil, *Spegazzini s.n.* (holotype, LPS 12515!; isotype, BAA!).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, Uruguay in the departments of Lavalleja, Maldonado, and Soriano, and Argentina in the provinces of Misiones and Buenos Aires. This species is frequent in rocky prairies, and in Brazil it grows in savannas.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

30. Piptochaetium sagasteguii Sánchez Vega, Arnaldoa 1(1): 17. 1991. TYPE: Peru. Cajamarca: Cerro El Guitarrero, ladera occidental del valle de Cajamarca, 2800 m, 15 Jan. 1983, *I. Sánchez Vega 2914* (holotype, CPUN!; isotypes, AAU not seen, CHAPA not seen, F not seen, HAO not seen, K not seen, MO!, US 3232467 not seen, USM not seen).

Distribution. Known from Peru in the departments of Cajamarca and La Libertad at elevations between 2700 and 3500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

31. Piptochaetium seleri (Pilger) Henrard, Blumea 3: 452. 1940. *Oryzopsis seleri* Pilg., Verh. Bot. Vereins Prov. Brandenburg 51: 192. 1909. TYPE: Guatemala. Huehuetenango: between Todos los Santos and Chiantla, 3000 m, Sep.?, *Seler 3238* (holotype, B not seen; isotypes, BAA!, US 2767420 not seen). Figure 5F.

Plants perennial. *Culms* 20–90 cm tall, terete, glabrous; nodes 2 or 3, reddish, compressed, glabrous; internodes (4.5–)10–15 cm long. *Leaf sheaths* embracing the culms, generally shorter than the internodes, 8–9 cm long, glabrous. *Ligules* 0.8–2 mm long, blunt to subacute, membranous, margins entire, glabrous. *Leaf blades* linear, convolute, 5.5–12 cm long, 0.4–0.5 mm wide, abaxial side scabrous on the nerves, adaxial side glabrous. *Peduncles* terete, 22–26 cm long, longitudinally striate, glabrous. *Inflorescences* 7–22 cm long, few to many flowered (25 to 60 spikelets), with branches loosely disposed; pedicels angled, 0.4–1.5 cm long, glabrous. *Spikelets* fusiform, 4–5 mm long, 1–1.4 mm diam. *Glumes* subequal, longer than the floret, 4–5 mm long, shortly acuminate, 5-nerved, violaceous, hyaline toward the margin. *Floret* terete, slightly obovoid, 3–4.5 mm long, 1–1.2 mm diam. *Lemma* narrowed below the crown, 3–4.5 mm long, striate, with short macrohairs and hooks all over the surface; crown contracted at the base of the awn, straight, not revolute, 0.4–0.5 mm diam., with prickles and short macrohairs; callus 0.4–0.6 mm long, blunt, obliquely truncate, hairy, the hairs slightly longer than the callus; awn bigeniculate, 1–1.5 cm long, persistent, shortly hispid. *Palea* ca. 3.5 mm long. *Lodicules* 2, 0.8–1 mm long, acute. *Caryopsis* terete, slightly obovoid, 3–3.2 mm long, 0.8–0.9 mm diam.; hilum linear; embryo ¼ the length of the caryopsis.

Distribution. Widespread in Mexico and southern Guatemala, between 2000 and 3600 m.

Selected specimens examined. MEXICO. **Coahuila:** Cañón de San Lorenzo, Sierra de Zapalinamé, 3 km S of Saltillo, *Snow et al. 6721* (MO). **Distrito Federal:** Desierto de los Leones, *Lyonnet 2719* (US); lava fields ca. 2 km SSW of La Cima, R.R. station on either side of old hwy. 95, 14 Aug. 1960, *Iltis et al. 958* (US). **Hidalgo:** woodlands near Trinidad Iron Works, *Pringle 13249* (MO, US). **México:** Sierra de Las Cruces, *Pringle 5200* (MEXU, US); 10 km al E de Amecameca, sobre la carretera a Tlamacas, 13 Nov. 1977, *Rzedowski 35555* (MEXU); 27 km SW of Toluca on road to Temaxcaltepic, *Mick & Roe 180* (US); Llano Grande, *Matuda 19202* (MEXU); Llano Grande, near Río Río, *Sharp 44144* (US); Chapingo, Ixtapaluca, faldas del Cerro El Papayo, Campo Experimental Zoquiapán, *Zavala Ch. 245* (XAL); al SW del Centro Experimental Zoquiapán, *Velazco Torres & J. Trinidad s.n.* (XAL); Telapon, *Lyonnet & Elcoro 1948* (US); Parque Nacional Lagunas de Zempoala, *Traylor 61* (MEXU, US). **Michoacán:** Santa Clara del Cobre, Laguna de San Gregorio, *Escobedo 1478* (XAL); summit of Cerro San Andres, ca. 12 km N of Ciudad Hidalgo, *Beaman 4273*, *Beaman 4329* (US). **Morelos:** Zempoala, *Lyonnet 2511* (MEXU). **Oaxaca:** 18 mi. SW of city of Oaxaca, *Nelson 1373 a* (US). **Tlaxcala:** ca. 3 mi. NE of Tlaxco, *Sohns 604* (US). **Veracruz:** Acajete, *Rzedowski 11940* (MEXU); Calcahualco, end of passable portion of road from Coscomatepec-Escola-Jacal to Miguel Hidalgo and Tlachichuca, *Nee & Diggs 24775* (MO, XAL); La Joya, *Mejía S. 218* (XAL); Las Minas, vereda de Cruz Blanca a Rinconado, *Durán E. & Burgos 498* (XAL); Las Vigas, 1 km despues de pasar la presa del Alto Pixquiac rumbo a Tembladeras, *Chazaro & Robles 3792* (XAL); Manzanares, Las Vigas, *Ventura A. 18506* (XAL); Perote, Escobillo, *Sandoval 68* (XAL); Perote, por la brecha que va a Tonalaco en las faldas del Cofre de Perote, *Castillo et al. 1980* (XAL); Soledad Atzompa, *Martínez & Acosta P. 1063* (XAL); Xico, Tonalaquillo, *Arriaga C. 351* (XAL). GUATEMALA. **Huehuetenango:** Sierra de los Cuchumatanes, immediately N of Tojiah at km 322, on ruta nacional 9 N, *Beaman 3928* (US); near Tunimá, Sierra de los Cuchumatanes, *Steyermark 48274* (US); trail between Soloma and Santa Eulalia, Sierra de los Cuchumatanes, *Steyermark 48452* (US). **Totonicapán:** Desconsuelo, potrero natural, flora alpina, *de Koninck 114* (US); on the Tecum Uman Ridge at km 154 on ruta nacional nro. 1, ca. 20 km E of Totonicapán, *Beaman 4155* (US).

Beetle (1977) and Hitchcock (1951, under *Oryzopsis seleri*) placed *Piptochaetium seleri* in synonymy with *P. fimbriatum*. Both species have terete, slightly obovoid florets and lemma with macrohairs, but *P. fimbriatum* has smooth or thinly striate lemmas, without prickles or hooks, and a crown without epidermal appendages.

32. Piptochaetium setosum (Trinius) Arechavaleta, Anales Mus. Nac. Montevideo 1: 330. 1896. *Urachne setosa* Trin., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 6(1): 124. 1834, nom illeg. superfl. TYPE: Chile. Without locality, *Cumming s.n.*, TRIN 1473.1 (lectotype, designated by Parodi (1944), LE not seen; isotype, US not seen).

Urachne fusca Nees ex Steud., Syn. Pl. Glumac. 1: 123. 1854. TYPE: Chile. Valparaíso: *Cumming 453* (isotype, K!).

Piptochaetium purpuratum Phil., Linnaea 29: 86. 1857. TYPE: "Chile. Valparaíso, Nov. 1854" (probable holotype, SGO 57419!).

Piptochaetium pallidum Phil. ex Griseb., Symb. Fl. Argent.: 279. 1879. TYPE: Chile. Cerro San Cristóbal, *Philippi s.n.* (lectotype, designated here, SGO 57412!).

Piptochaetium macrocarpum Phil., Anales Univ. Chile 93: 735. 1896. TYPE: Chile. Ñuble, *N. Briones s.n.* (holotype, SGO 45082!).

Distribution. This species presents, at the moment, a disjunct distribution in southern North America (California) and South America (Bark-

31. Piptochaetium seleri (Pilger) Henrard, Blumea 3: 452. 1940. *Oryzopsis seleri* Pilg., Verh. Bot. Vereins Prov. Brandenburg 51: 192. 1909. TYPE: Guatemala. Huehuetenango: between Todos los Santos and Chiantla, 3000 m, Sep.?, *Seler 3238* (holotype, B not seen; isotypes, BAA!, US 2767420 not seen). Figure 5F.

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Distribution. This species presents, at the moment, a disjunct distribution in southern North America (California) and South America (Barkworth, 1986, 1993), where it grows in central Chile from Valparaíso to Valdivia.

Observation. This species has a strikingly prostrate habit in some specimens collected in California (Barkworth, pers. comm.).

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. *Piptochaetium setosum* (Trin.) Arechav. was based on *Urachne setosa* Trin., a nomenclaturally superfluous name when published, as Trinius cited *Stipa panicoides* Lam. and *Oryzopsis setacea* A. Rich. as synonyms, both earlier published. Nevertheless, *P. setosum* is the correct name in *Piptochaetium* for *Urachne setosa* when *Stipa panicoides* and *Oryzopsis setacea* are considered synonyms of another species, *Piptochaetium panicoides* (Lam.) E. Desv.

33. Piptochaetium stipoides (Trinius & Ruprecht) Hackel, Anales Mus. Nac. Montevideo 1(4): 328. 1896.

33a. Piptochaetium stipoides (Trinius & Ruprecht) Hackel var. **stipoides.** *Urachne stipoides* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg, sér. 6, Sci. Nat. 5: 25. 1842. *Oryzopsis stipoides* (Trin. & Rupr.) Speg., Anales Mus. Nac. Montevideo 4(2): 23. 1901. *Piptochaetium stipoides* (Trin. & Rupr.) Hack. var. *genuinum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 266. 1944, nom. inval. TYPE: Brazil. Brasilia meridionalis, *Sellow s.n.* (holotype, LE not seen).

Piptochaetium chaetophorum Griseb., Symb. Fl. Argent.: 298. 1879. *Piptochaetium ovatum* E. Desv. var. *chaetophorum* (Griseb.) Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 104. 1904. TYPE: Argentina. Córdoba: Dpto. Punilla, Pan de Azúcar, *Hieronymus s.n.*, *Herb. Grisebach 253* (holotype, GOET not seen; isotype, CORD!).

Piptochaetium cuspidatum Phil., Anales Univ. Chile 93: 732. 1896. TYPE: Chile. Salto de Conchalí, *Philippi s.n.* (holotype, SGO 57401!; isotype, US 1819510 not seen).

Piptochaetium ovatum E. Desv. var. *purpurascens* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 86. 1911. *Piptochaetium stipoides* (Trin. & Rupr.) Hack. var. *purpurascens* (Hack.) Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 272. 1944. TYPE: Argentina. Chaco: Dpto. 1 de Mayo, Margarita Belén, *Stuckert 19189* (lectotype, here designated, CORD!).

Piptochaetium ovatum E. Desv. f. *atrata* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 85. 1911. TYPE: Argentina. Chaco: Dpto. 1 de Mayo, Colonia Benítez, *Stuckert 18304* (holotype, W not seen; isotype, CORD!).

Stipa verruculosa Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 206. 1921. *Piptochaetium verruculosum* (Mez) Henrard, Meded. Rijks-Herb. 54: 380. 1927. *Piptochaetium verruculosum* (Mez) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940, comb. superfl. TYPE: Argentina. Buenos Aires: without locality, *Balansa s.n.* (holotype, B not seen; isotype, US not seen).

Piptochaetium grisebachi (Speg.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. *Oryzopsis grisebachi* Speg., Anales Mus. Nac. Montevideo 4(2): 4. 1901. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, *Lorentz s.n.*, Flora Entrerriana 1691 (holotype, CORD!; isotype, LPS!).

Piptochaetium stipoides (Trin. & Rupr.) Hack. var. *parviflorum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 275. 1944. TYPE: Argentina. Buenos Aires: Pdo. Balcarce, Balcarce, *Martínez Crovetto 950 1/2* (holotype, BAA!).

Distribution. This variety presents, at the moment, a disjunct distribution (Thomasson, 1980; Barkworth, 1986, 1993) in the southwestern United States and Mexico (Beetle, 1977), and in South America, where it grows in southern Brazil in the states of Rio Grande do Sul and Santa Catarina. It is also widespread in Uruguay, in Canelones, Colonia, Flores, Florida, Lavalleja, Montevideo, Paysandú, Río Negro, Salto, Soriano, and Tacuarembó; in Chile, in VIII and IX Regions and in Región Metropolitana; and in Argentina in the provinces of Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Jujuy, Misiones, Río Negro, and Santa Fe. This variety is known up to elevations of 2000 m in arid regions.

Additional specimens examined. ARGENTINA. **Chaco:** Margarita Belén, 1 Nov. 1908, *Stuckert 19208* (CORD). MEXICO. **Tamaulipas:** Sierra de San Carlos, Cerro de los Armadillos, 10 July 1930, *Bartlett 10225* (US).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

33b. Piptochaetium stipoides (Trinius & Ruprecht) Hackel var. **echinulatum** Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 271. 1944. TYPE: Argentina. Buenos Aires: Pdo. Puán, Villa Iris, *Parodi 13759* (holotype, BAA!).

The florets of this variety present the lemma with prickles partially covered by adjacent epidermal cells at the base (Cialdella & Arriaga, 1998: figs. 3D, 10J).

Distribution. This variety has been found in central Argentina in the provinces of Buenos Aires, La Pampa, and San Luis, and in northern Uruguay in the department of Salto.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

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Observation. This species has a strikingly prostrate habit in some specimens collected in California (Barkworth, pers. comm.).

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Note. *Piptochaetium setosum* (Trin.) Arechav. was based on *Urachne setosa* Trin., a nomenclaturally superfluous name when published, as Trinius cited *Stipa panicoides* Lam. and *Oryzopsis setacea* A. Rich. as synonyms, both earlier published. Nevertheless, *P. setosum* is the correct name in *Piptochaetium* for *Urachne setosa* when *Stipa panicoides* and *Oryzopsis setacea* are considered synonyms of another species, *Piptochaetium panicoides* (Lam.) E. Desv.

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Piptochaetium grisebachi (Speg.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. *Oryzopsis grisebachi* Speg., Anales Mus. Nac. Montevideo 4(2): 4. 1901. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, *Lorentz s.n.*, Flora Entrerriana 1691 (holotype, CORD!; isotype, LPS!).

Piptochaetium stipoides (Trin. & Rupr.) Hack. var. *parviflorum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 275. 1944. TYPE: Argentina. Buenos Aires: Pdo. Balcarce, Balcarce, *Martínez Crovetto 950 1/2* (holotype, BAA!).

Distribution. This variety presents, at the moment, a disjunct distribution (Thomasson, 1980; Barkworth, 1986, 1993) in the southwestern United States and Mexico (Beetle, 1977), and in South America, where it grows in southern Brazil in the states of Rio Grande do Sul and Santa Catarina. It is also widespread in Uruguay, in Canelones, Colonia, Flores, Florida, Lavalleja, Montevideo, Paysandú, Río Negro, Salto, Soriano, and Tacuarembó; in Chile, in VIII and IX Regions and in Región Metropolitana; and in Argentina in the provinces of Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Jujuy, Misiones, Río Negro, and Santa Fe. This variety is known up to elevations of 2000 m in arid regions.

Additional specimens examined. ARGENTINA. **Chaco:** Margarita Belén, 1 Nov. 1908, *Stuckert 19208* (CORD). MEXICO. **Tamaulipas:** Sierra de San Carlos, Cerro de los Armadillos, 10 July 1930, *Bartlett 10225* (US).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

33b. Piptochaetium stipoides (Trinius & Rupprecht) Hackel var. **echinulatum** Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 271. 1944. TYPE: Argentina. Buenos Aires: Pdo. Puán, Villa Iris, *Parodi 13759* (holotype, BAA!).

The florets of this variety present the lemma with prickles partially covered by adjacent epidermal cells at the base (Cialdella & Arriaga, 1998: figs. 3D, 10J).

Distribution. This variety has been found in central Argentina in the provinces of Buenos Aires, La Pampa, and San Luis, and in northern Uruguay in the department of Salto.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

34. Piptochaetium tovarii Sánchez Vega, Arnaldoa 1(1): 25. 1991. TYPE: Peru. Cajamarca: Cajamarca, entre Cajamarca y Cumbemayo, Fundo Universidad, 3450 m, 22 May 1971, *I. Sánchez Vega & N. Vilhena 678* (holotype, CPUN!; isotypes, MO!, US 3232468 not seen).

Distribution. Southern Ecuador in the limited region between provinces of Loja and Azuay, and northwestern Peru in the departments of Piura, Cajamarca, and Ancash, at elevations between 2700 and 3450 m.

Additional specimens examined. ECUADOR. **Azuay-Loja:** Nudo de cordillera occidental y cordillera oriental, entre Oña y Rancho Ovejero, 1–2 Aug. 1959, *Barclay & Juajibioy 8455* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

35. Piptochaetium uruguense Grisebach, Symb. Fl. Argent.: 297. 1879. *Oryzopsis uruguayensis* (Griseb.) Speg., Anales Mus. Nac. Montevideo 4(2): 29. 1901. *Piptochaetium uruguense* Griseb. var. *genuinum* Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 290. 1944, nom. inval. TYPE: Argentina. Entre Ríos: Dpto. Uruguay, Concepción del Uruguay, 13 Nov. 1875, *P. G. Lorentz 471* (holotype, probably in GOET not seen; isotypes, BA!, CORD!).

Piptochaetium uruguense Griseb. var. *microcarpum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 290. 1944. TYPE: Argentina. Corrientes: Dpto. San Martín, Yapeyú, *Parodi 12637* (holotype, BAA!).

Distribution and ecology. For the time being, this species presents a disjunct distribution in Mexico (Thomasson, 1980; Barkworth, 1986) and in South America, in Paraguay, departments of Misiones and Guairá, in western Uruguay, departments of Cerro Largo, Flores, Florida, Paysandú, and Rocha, and in northern and northeastern Argentina, provinces of Chaco, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. *Piptochaetium uruguense* also grows in southern Brazil, state of Rio Grande do Sul, and it has been cited for Santa Catarina (Smith et al., 1982). This species grows in wet prairies.

Additional specimen examined. BRAZIL. **Rio Grande do Sul:** Fazenda Experimental de Criacao Bage, 1 Dec. 1945, *Swallen 7561* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

36. Piptochaetium virescens (Kunth) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 230. 1944. *Stipa virescens* Kunth, Nov. Gen. Sp. 1: 126. 1816. TYPE: Mexico. Guanajuato, Santa Rosa, Cuesta de Belgrado y La Buffa, *Humboldt & Bonpland s.n.* (holotype, P not seen; isotype, US 00141712 not seen). Figure 5C.

Stipa arsenii Hack., Repert. Spec. Nov. Regni Veg. 8: 515. 1910. *Piptochaetium virescens* (Kunth) Parodi var. *arsenii* (Hack.) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico. Michoacán: Morelia, 2200 m, *Fr. Arsène 3211* (holotype, W not seen; isotypes, US not seen, MO 845899 not seen).

Plants perennial. *Culms* 0.70–1.30 m tall, terete, glabrous, occasionally hispidous below the nodes; nodes 3 or 4, brownish, compressed, glabrous; internodes 12–45 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 9.5–15 cm long, glabrous. *Ligules* 1–2.5 mm long, blunt, margins entire, glabrous, sometimes hispidous at the abaxial side. *Leaf blades* linear, convolute, 10–35 cm long, 0.5–1 mm wide, longitudinally striate, glabrous, scabrous at the margins. *Peduncles* terete, 40–44 cm long, longitudinally ribbed, glabrous. *Inflorescences* 10–30 cm long, many-flowered (25 to 80 spikelets), with branches loosely disposed; pedicels slightly angled, 2–18 mm long, hispid. *Spikelets* fusiform, 6–8 mm long, 1.2–1.4 mm diam. *Glumes* subequal, longer than the floret, 6–8.5 mm long, shortly acuminate, 5-nerved, hyaline toward the margins. *Floret* terete-fusiform, 5.5–8(–9) mm long, 1 mm diam. *Lemma* slightly contracted below the crown, 5.5–8 mm long, thinly striate, with hooks and macrohairs uniformly disposed; crown contracted at the base of the awn, straight, not revolute, 0.5–0.7 mm diam., with prickles and rows of macrohairs 0.5–0.6 mm long, occasionally 1 mm long; callus 0.9–1 mm long, acute, occasionally subacute, densely hairy, the upper macrohairs slightly longer than the callus; awn bigeniculate, 13–20 mm long, persistent, hispid, scabrous toward the apex. *Palea* ca. 5 mm long. Lodicules 2, 1.4–1.6 mm long, acute. *Caryopsis* terete, 3–3.2 mm long, 0.9 mm diam.; hilum linear; embryo ⅙ the length of the caryopsis.

Chromosome numbers. $2n$ = ca. 60 (Gould, 1966, as *Stipa virescens*).

Distribution. Guatemala and central and southern Mexico. This species was cited also for Venezuela, Barinas, in TROPICOS based on *J. Brunken & C. Perino 355* (MO), which we did not see.

Selected specimens examined. GUATEMALA. **Huehuetenango:** Cumbre Papal, between summit and La Libertad, *Steyermark 50955* (US). **Quezaltenango:** La Es-

34. Piptochaetium tovarii Sánchez Vega, Arnaldoa 1(1): 25. 1991. TYPE: Peru. Cajamarca: Cajamarca, entre Cajamarca y Cumbemayo, Fundo Universidad, 3450 m, 22 May 1971, *I. Sánchez Vega & N. Vilhena 678* (holotype, CPUN!; isotypes, MO!, US 3232468 not seen).

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Distribution and ecology. For the time being, this species presents a disjunct distribution in Mexico (Thomasson, 1980; Barkworth, 1986) and in South America, in Paraguay, departments of Misiones and Guairá, in western Uruguay, departments of Cerro Largo, Flores, Florida, Paysandú, and Rocha, and in northern and northeastern Argentina, provinces of Chaco, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. *Piptochaetium uruguense* also grows in southern Brazil, state of Rio Grande do Sul, and it has been cited for Santa Catarina (Smith et al., 1982). This species grows in wet prairies.

Additional specimen examined. BRAZIL. **Rio Grande do Sul:** Fazenda Experimental de Criacao Bage, 1 Dec. 1945, *Swallen 7561* (MO).

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Stipa arsenii Hack., Repert. Spec. Nov. Regni Veg. 8: 515. 1910. *Piptochaetium virescens* (Kunth) Parodi var. *arsenii* (Hack.) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico. Michoacán: Morelia, 2200 m, *Fr. Arsène 3211* (holotype, W not seen; isotypes, US not seen, MO 845899 not seen).

Plants perennial. *Culms* 0.70–1.30 m tall, terete, glabrous, occasionally hispidous below the nodes; nodes 3 or 4, brownish, compressed, glabrous; internodes 12–45 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 9.5–15 cm long, glabrous. *Ligules* 1–2.5 mm long, blunt, margins entire, glabrous, sometimes hispidous at the abaxial side. *Leaf blades* linear, convolute, 10–35 cm long, 0.5–1 mm wide, longitudinally striate, glabrous, scabrous at the margins. *Peduncles* terete, 40–44 cm long, longitudinally ribbed, glabrous. *Inflorescences* 10–30 cm long, many-flowered (25 to 80 spikelets), with branches loosely disposed; pedicels slightly angled, 2–18 mm long, hispid. *Spikelets* fusiform, 6–8 mm long, 1.2–1.4 mm diam. *Glumes* subequal, longer than the floret, 6–8.5 mm long, shortly acuminate, 5-nerved, hyaline toward the margins. *Floret* terete-fusiform, 5.5–8(–9) mm long, 1 mm diam. *Lemma* slightly contracted below the crown, 5.5–8 mm long, thinly striate, with hooks and macrohairs uniformly disposed; crown contracted at the base of the awn, straight, not revolute, 0.5–0.7 mm diam., with prickles and rows of macrohairs 0.5–0.6 mm long, occasionally 1 mm long; callus 0.9–1 mm long, acute, occasionally subacute, densely hairy, the upper macrohairs slightly longer than the callus; awn bigeniculate, 13–20 mm long, persistent, hispid, scabrous toward the apex. *Palea* ca. 5 mm long. Lodicules 2, 1.4–1.6 mm long, acute. *Caryopsis* terete, 3–3.2 mm long, 0.9 mm diam.; hilum linear; embryo $\frac{1}{6}$ the length of the caryopsis.

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Selected specimens examined. GUATEMALA. **Huehuetenango:** Cumbre Papal, between summit and La Libertad, *Steyermark 50955* (US). **Quezaltenango:** La Esperanza, *De Koninck 73 A and B* (US). **San Marcos:** Barrancos 6 mi. S and W of town of Tajumulco, NW slopes of Volcán Tajumulco, *Steyermark 36700* (US). MEXICO. **Chiapas:** SW of Mexican hwy. 190 near Rancho Nuevo, about 9 mi. SE of San Cristóbal las Casas, *Breedlove 14171* (US). **Distrito Federal:** Valle de Mexico, C. de Ajusco, *Matuda 25753* (MEXU); S. de Ajusco, *Pringle 6588* (MEXU, MO, US); Cerro Magdalena, Serranía de Ajusco, *Lyonnet 1877* (MO); 4 km W of San Andreas, Pedregal de San Angel, *Sohns 177* (US). **Hidalgo:** Tepeapulco, Cerro de Xihuingo, *Ventura A. 376* (MO); Tulancingo, open pine woods near reservoir at Tejocotal between Acaxochitlan and Puebla, *Moore Jr. 2843* (US); Real de Monte, *Matuda 18907* (US). **Jalisco:** 14–18 km SW of Tequila on Volcán de Tequila, *Breedlove 39241* (MO); Zapotlán, *Hitchcock 7169* (US); Sierra del Tigre, 3 mi. S of Mazamitla, *McVaugh 12268* (US); volcano of Colima, *Jones 479* (US). **México:** Valle de Mexico, C. Benacho, cerca de Amecameca, *Matuda 25724* (MEXU, MO); Ixtapaluca, 8 km S de Río Frío, *Koch 762* (MO); Popo Park, *Hitchcock 5965* (US); Cerro de Pinal, Otzoloapan, *Matuda et al. 31875* (US). **Michoacán:** in open pine forest and in open areas in and around the NE side of the Volcán de Paricutin, *Sohns 819* (MEXU); ca. 18 mi. S of Patzcuaron, *King & Soderstrom 5151* (MEXU); Las Cañas, *Rzedowski & McVaugh 623* (MO); Las Cañas, estribaciones inferiores noroccidentales del Cerro Patamban, Tangancicuaro, *Rzedowski & McVaugh 623* (US). **Morelos:** Sierra de Ajusco, *Pringle 6236* (MEXU, MO, US); Lagunas Zempoala, *Lyonnet 2498* (US). **Oaxaca:** 23 km de Tlaxiaco, rumbo a Chalcotongo, *Beetle M-4743* (MO); 0.5 km E de Las Huertas, Nundichi, Tlaxiaco, *Manzanero M. 450* (MO); 1 km al S de San Andrés, carr. Oaxaca–Puerto Angel, Miahuatlan, *Torres & Cedillo 875* (MO). **Puebla:** 8 ó 9 km al N de Tlaxco, al S de Cerro La Paila, *Chimal et al. 9* (MO); 5 mi. NE of Zacatepec, on hwy. 40 from Jalapa, *Soderstrom 493* (US); in pine forest, near crest of road pass, 46 mi. NW of Puebla on old hwy. to Mexico City, *Gould 10183* (US). **San Luis Potosí:** on the NE slopes of hills near Aguaje de García in the Sierra de Guadalcazar, *Sohns 1500* (US). **Tlaxcala:** Huamantla, 500 m al SW de Altamirano Guadalupe, *Guerrero et al. 632* (MO); 3 mi. NE of Tlaxco, *Sohns 601*, *Sohns 603* (US). **Veracruz:** Ayahualulco, *Nee 22928* (MO). **Zacatecas:** collected near Plateado, *Rose 2750* (US).

Piptochaetium virescens is similar to *P. indutum*: they share the floret and callus shape and the epidermal appendages on the lemma. *Piptochaetium indutum* can be recognized because it includes smaller plants, 15–35 cm tall, with smaller florets, (4–)5–6.25 mm long and 1 mm diam., with longer glumes, (7–)8–13.5 mm.

Piptochaetium virescens and *P. sagasteguii* are also related species, with similar floret characters; *P. sagasteguii* may be recognized because it includes smaller plants, 25–65 cm tall, with few-flowered inflorescences of 15 to 22 spikelets. The geographical distribution of these species is also different: *P. sagasteguii* is only known for Peru, while *P. virescens* can be found in Mexico and Guatemala.

EXCLUDED SPECIES FROM *PIPTOCHAETIUM*

Piptochaetium mexicanum (Hitchc.) Beetle, Phytologia 54: 4. 1983 = *Nassella mexicana* (Hitchc.) Pohl, Taxon 39: 611. 1990. [Basionym: *Stipa mexicana* Hitchc., Contr. U.S. Natl. Herb. 24: 247. 1925.]

NOMINA NUDA

Podopogon avenaceus Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. = *Piptochaetium avenaceum* (L.) Parodi.

Podopogon barbatus Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. = *Piptochaetium avenaceum* (L.) Parodi.

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Piptatherum elegans P. Beauv., Essai Agrost.: 173. 1812, nom. nud. = *Piptochaetium panicoides* (Lam.) E. Desv.

Piptatherum panicoides Gilbert, Enum. Pl. Montev.: 117. 1873, nom. nud. = *Piptochaetium panicoides* (Lam.) E. Desv.

Piptatherum stipoides Gilbert, Enum. Plant. Montev.: 117. 1873, nom. nud. = *Piptochaetium stipoides* (Trin. & Rupr.) var. *stipoides*.

Literature Cited

Barkworth, M. E. 1986. *Piptochaetium* Presl (Gramineae, Stipeae) in North and Mesoamerica: Taxonomic and distributional observations. Brenesia 25–26: 169–178.

———. 1988. New taxa in *Piptochaetium* (Stipeae, Gramineae) from Mexico. Syst. Bot. 13: 196–201.

———. 1990. *Nassella* (Gramineae, Stipeae): Revised interpretation and nomenclatural changes. Taxon 39: 597–614.

———. 1993. North American Stipeae (Gramineae): Taxonomic changes and other comments. Phytologia 74: 1–25.

Beetle, A. A. 1977. Noteworthy grasses from Mexico V. Phytologia 37: 317–407.

Brako, L. & J. L. Zarucchi. 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru/Catálogo de las Angiospermas y Gimnospermas del Perú. Monogr. Syst. Bot. Missouri Bot. Gard. 45.

Bremer, K. 1988. The limits of amino acid sequence data in Angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brown, W. V. 1951. Chromosome numbers of some Texas grasses. Bull. Torrey Bot. Club 78: 292–299.

Cialdella, A. M. & M. Arriaga. 1998. Revisión de las especies sudamericanas del género *Piptochaetium* (Poaceae, Pooideae, Stipeae). Darwiniana 36: 107–157.

Clayton, W. D. 1983. Proposal to conserve 212 *Pipto-*

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Literature Cited

Barkworth, M. E. 1986. *Piptochaetium* Presl (Gramineae, Stipeae) in North and Mesoamerica: Taxonomic and distributional observations. Brenesia 25–26: 169–178.

———. 1988. New taxa in *Piptochaetium* (Stipeae, Gramineae) from Mexico. Syst. Bot. 13: 196–201.

———. 1990. *Nassella* (Gramineae, Stipeae): Revised interpretation and nomenclatural changes. Taxon 39: 597–614.

———. 1993. North American Stipeae (Gramineae): Taxonomic changes and other comments. Phytologia 74: 1–25.

Beetle, A. A. 1977. Noteworthy grasses from Mexico V. Phytologia 37: 317–407.

Brako, L. & J. L. Zarucchi. 1993. Catalogue of the Flowering Plants and Gymnosperms of Peru/Catálogo de las Angiospermas y Gimnospermas del Perú. Monogr. Syst. Bot. Missouri Bot. Gard. 45.

Bremer, K. 1988. The limits of amino acid sequence data in Angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

———. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brown, W. V. 1951. Chromosome numbers of some Texas grasses. Bull. Torrey Bot. Club 78: 292–299.

Cialdella, A. M. & M. Arriaga. 1998. Revisión de las especies sudamericanas del género *Piptochaetium* (Poaceae, Pooideae, Stipeae). Darwiniana 36: 107–157.

Clayton, W. D. 1983. Proposal to conserve 212 *Pipto-*

chaetium K. B. Presl over *Podopogon* Rafin. (Gramineae). Taxon 32: 649.

Desvaux, E. 1853. Gramineae. *In* C. Gay (editor), Historia física y política de Chile 6: 233–551.

Elias, M. K. 1932. Grasses and other plants from the Tertiary rocks of Kansas and Colorado. Univ. Kansas Sci. Bull. 20: 333–367.

———. 1942. Tertiary Prairie Grasses and Other Herbs from the High Plains. Special Pap. Geol. Soc. Amer. 41. Nebraska Geological Survey, The University of Nebraska, Lincoln.

Ellis, R. P. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–671.

Goloboff, P. A. 1993a. NONA version 1.6 (32 bit). Computer software and manual. [Distributed by the author.]

———. 1993b. Estimating character weights during tree search. Cladistics 9: 83–91.

———. 1997. Pee-Wee version 2.8 (32 bit). Computer software and manual. [Distributed by the author.]

Gould, F. W. 1958. Chromosome numbers in Southwestern grasses. Amer. J. Bot. 45: 757–768.

———. 1966. Chromosome numbers of some Mexican grasses. Canad. J. Bot. 44: 1683–1696.

Hitchcock, A. S. 1923. New species of grasses from South America. Proc. Biol. Soc. Wash. 36: 195–198.

———. 1951. Manual of the Grasses of the United States, ed. 2, rev. by A. Chase. Misc. Publ. U.S. Dept. Agric. 200.

Holmgren, P. K., N. H. Holmgren & L. C. Barnett. 1990. Index Herbariorum. Part I: The Herbaria of the World. Regnum Veg. 120.

Jacobs, S. W. L., J. Everett & M. E. Barkworth. 1995. Classification of morphological terms used in the Stipeae (Gramineae), and a reassessment of *Nassella* in Australia. Taxon 44: 33–41.

Jørgensen, P. M. & S. León-Yánez (editors). 1999. Catalogue of the Vascular Plants of Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 75.

Metcalfe, C. R. 1960. Anatomy of the Monocotyledons. I. Gramineae. Clarendon Press, Oxford.

Muñoz-Schick, M. 1990. Revisión del género *Nassella* (Trin.) E. Desv. (Gramineae) en Chile. Gayana, Bot. 47: 9–35.

Myers, W. M. 1947. Cytology and genetics of forage grasses. Bot. Rev. 13: 319–422.

Parodi, L. R. 1944. Revisión de las gramíneas australes americanas del género *Piptochaetium*. Revista Mus. La Plata, secc. Bot. 6: 213–310.

———. 1961. Gramineas argentinas nuevas o críticas. III. Revista Argent. Agron. 28(3–4): 100–125.

Peñailillo, B. P. 1996. *Anatherostipa*, un nuevo género de Poaceae. Gayana, Bot. 53: 277–284.

Presl, C. B. 1830. Reliquiae Haenkeanae. J. C. Calve, Prague 1: 207–355.

Reeder, J. R. 1968. Notes on Mexican grasses VIII. Miscellaneous chromosome numbers—2. Bull. Torrey Bot. Club 95: 69–86.

———. 1977. Chromosome numbers in western grasses. Amer. J. Bot. 64: 102–110.

Sánchez Vega, I. 1991. Revisión de las especies peruanas del género *Piptochaetium* J. S. Presl (Gramineae). Arnaldoa 1: 11–34.

Smith, L. B., D. C. Wasshausen & R. M. Klein. 1982. Gramíneas. Gêneros: 45. *Deschampsia* até 84. *Pseudechinolaena*. *In* R. Reitz (editor), Flora Ilustrada Catarinense 1 (Gram.): 443–906.

Spegazzini, C. 1901. Stipeae Platenses. Anales Mus. Nac. Montevideo 4: 1–173.

Swallen, J. R. 1955. Flora of Guatemala 2: Grasses of Guatemala. Fieldiana Bot. 24: 1–390.

Thomasson, J. R. 1978a. Epidermal patterns of the lemma in some fossil and living grasses and their phylogenetic significance. Science 199: 975–977.

———. 1978b. Tertiary fossil plants found in Nebraska. Res. Rep. Natl. Geogr. Soc. 1978 Projects: 553–564.

———. 1980. Distribution in *Piptochaetium* (Gramineae–Stipeae): Paleophytogeographical significance. Iselya 1: 161–165.

———. 1982. Fossil grass anthoecia and other plant fossils from arthropod burrows in the Miocene of western Nebraska. J. Paleontology 56: 1011–1017.

———. 1985. Miocene fossil grasses: Possible adaptation in reproductive bracts (lemma and palea). Ann. Missouri Bot. Gard. 72: 843–851.

Torres, M. A. 1969. Nota sobre una especie de *Piptochaetium* de Argentina y Uruguay. Bol. Soc. Argent. Bot. 11: 251–254.

———. 1997. *Nassella* (Gramineae) del noroeste de la Argentina, *Stipa* (Gramineae) del noroeste de la Argentina, *Nicoraella* (Gramineae) un nuevo género para América del Sur. *In:* Ministerio de la producción y el empleo, provincia de Buenos Aires, Comisión de Investigaciones Científicas (CIC), Monografía 13: 3–76.

Valencia, J. I. & M. Costas. 1968. Estudios citotaxonómicos sobre *Piptochaetium* (Gramineae). Bol. Soc. Argent. Bot. 12: 168–179.

APPENDIX 1

Examined material of *Piptochaetium*. Each specimen is cited by the last name of the first collector when there is more than one collector. Species number is indicated between parentheses.

1. *Piptochaetium alpinum* L. B. Smith
2. *Piptochaetium angolense* Philippi
3. *Piptochaetium angustifolium* (Hitchcock) Valencia & Costas
4. *Piptochaetium avenaceum* (L.) Parodi
5. *Piptochaetium avenacioides* (Nash) Valencia & Costas
6. *Piptochaetium bicolor* (Vahl) E. Desvaux
7. *Piptochaetium brachyspermum* (Spegazzini) Parodi
8. *Piptochaetium brevicalyx* (E. Fournier) Ricker
9. *Piptochaetium burkartianum* Parodi
10. *Piptochaetium cabrerae* Parodi
11. *Piptochaetium calvescens* Parodi
12. *Piptochaetium confusum* Parodi
13. *Piptochaetium cucullatum* Rosengurtt & Izaguirre de Arturio
14. *Piptochaetium featherstonei* (Hitchcock) Tovar
15. *Piptochaetium fimbriatum* (Kunth) Hitchcock
16. *Piptochaetium hackelii* (Arechavaleta) Parodi
17. *Piptochaetium hirtum* Philippi
18. *Piptochaetium indutum* Parodi
19. *Piptochaetium jubatum* Henrard
20. *Piptochaetium lasianthum* Grisebach
21. *Piptochaetium lejopodum* (Spegazzini) Henrard
22. *Piptochaetium medium* (Spegazzini) Torres
23. *Piptochaetium montevidense* (Sprengel) Parodi
24. *Piptochaetium napostaense* (Spegazzini) Hackel
25. *Piptochaetium palustre* Mujica-Sallés & Longhi-Wagner
26. *Piptochaetium panicoides* (Lamarck) E. Desvaux

chaetium K. B. Presl over *Podopogon* Rafin. (Gramineae). Taxon 32: 649.

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Elias, M. K. 1932. Grasses and other plants from the Tertiary rocks of Kansas and Colorado. Univ. Kansas Sci. Bull. 20: 333–367.

———. 1942. Tertiary Prairie Grasses and Other Herbs from the High Plains. Special Pap. Geol. Soc. Amer. 41. Nebraska Geological Survey, The University of Nebraska, Lincoln.

Ellis, R. P. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12: 641–671.

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———. 1993b. Estimating character weights during tree search. Cladistics 9: 83–91.

———. 1997. Pee-Wee version 2.8 (32 bit). Computer software and manual. [Distributed by the author.]

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———. 1951. Manual of the Grasses of the United States, ed. 2, rev. by A. Chase. Misc. Publ. U.S. Dept. Agric. 200.

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———. 1961. Gramineas argentinas nuevas o críticas. III. Revista Argent. Agron. 28(3–4): 100–125.

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8. *Piptochaetium brevicalyx* (E. Fournier) Ricker
9. *Piptochaetium burkartianum* Parodi
10. *Piptochaetium cabrerae* Parodi
11. *Piptochaetium calvescens* Parodi
12. *Piptochaetium confusum* Parodi
13. *Piptochaetium cucullatum* Rosengurtt & Izaguirre de Arturio
14. *Piptochaetium featherstonei* (Hitchcock) Tovar
15. *Piptochaetium fimbriatum* (Kunth) Hitchcock
16. *Piptochaetium hackelii* (Arechavaleta) Parodi
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18. *Piptochaetium indutum* Parodi
19. *Piptochaetium jubatum* Henrard
20. *Piptochaetium lasianthum* Grisebach
21. *Piptochaetium lejopodum* (Spegazzini) Henrard
22. *Piptochaetium medium* (Spegazzini) Torres
23. *Piptochaetium montevidense* (Sprengel) Parodi
24. *Piptochaetium napostaense* (Spegazzini) Hackel
25. *Piptochaetium palustre* Mujica-Sallés & Longhi-Wagner
26. *Piptochaetium panicoides* (Lamarck) E. Desvaux

27. *Piptochaetium pilosum* (Sánchez Vega) Cialdella & Giussani
28. *Piptochaetium pringlei* (Beal) Parodi
29. *Piptochaetium ruprechtianum* E. Desvaux
30. *Piptochaetium sagasteguii* Sánchez Vega
31. *Piptochaetium seleri* (Pilger) Henrard
32. *Piptochaetium setosum* (Trinius) Arechavaleta
33. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel
33a. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel var. *stipoides*
33b. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel var. *echinulatum* Parodi
34. *Piptochaetium tovarii* Sánchez Vega
35. *Piptochaetium uruguense* Grisebach
36. *Piptochaetium virescens* (Kunth) Parodi

Aleman 267 (26); Alonso J. 151 (20); Andrews s.n. (4); Arriaga C. 351 (31); Arzivenco 349 (20), 352 (28).

Baker 115 (5), 1155 (5); Banda 132 (8); Barclay 8455 (34); Barkley 14 A 660 (15); Bartlett 10225 (33a); Bartley 2011 (4); Beaman 3928 (31), 4155 (31), 4273 (31), 4329 (31), 4387 (36); Beetle M-141 (36), M-4743 (36), M-7086 (36), M-7338 (15), M-7742 (15), M-7856 (28), M-7864 (15); Berkley 1579 (4); Biswell 94408 (4); Boechat 160 (28), 161 (20); Bonner 354 (4); Boott s.n. (4); Boufford 18242 (4); Bozeman 8842 (4); Brandegee 31 (15), 34 (15); Brant 2239 (15); Braun 1422 (4), 942 (4); Breedlove 14171 (36), 39241 (36), 43293 (15), 44133 (15); Bro. Arsène 2699 (36), 5305 (36), 5375 (36), 6749 (36); Brunken 234 (15), 247 (36), 387 (36); Burgess 227 (4).

Calzada 4645 (15); Carter 2396 (15); Castillo 1980 (31); Chapman 1037 (4); Chase 7220 (4), 7312 (4), 7401 (4); Chazaro 3792 (31); Chiang 9077 (15); Chimal 9 (36), 1954 (31); Churchill 123 (4), s.n. (4); Cole s.n. (4); Collins s.n. (4); Combo 876 (4); Commons 269 (4); Correll 353 (4), 13699 (15), 16170 (4); Cronquist 4311 (4), 4432 (4), 5014 (4), 5075 (4); Curtiss 5834 (5).

Darrow 1287 (15); Davidse 9287 (15), 9485 (15), 9832 (36), 10031 (15), 11137 A (33a), 29775 (15); De Chalmot s.n. (4); De Koninck 73 (36), 114 (31); Deam 20709 (4), 36302 (4), 40704 (4), 64413 (4); Demaree 14586 (4), 19003 (4), 63483 (4); Dowell 7309 (5); Duncan 9485 (4); Durán E. 498 (31).

Earle 165 (15); Early s.n. (4); Eggert 36 (4), s.n. (4); Egler 41–136 (4); Ellis 1113 (31); Escobedo 1478 (31).

Faircloth 5079 (4), 5798 (4), 7070 (4); Felger 92–794 (15); Fernald 7760 (4); Fernández 734 (28), 735 (20); Ferris 2736 (15), 2812 (15); Fisher 108 (31), s.n. (31), s.n. (4); Fogg Jr. 2224 (4); Fredholm 5092 (5), 5725 (5); Freeman 54117 (4).

Garber s.n. (4); Gentry 8492 (15); Gleason 8537 (4); Godfrey 3686 (4), 8085 (4), 67795 (4); Gould 2456 (28), 3768 (28), 4419 (15), 9211 (8), 9602 (15), 9661 (15), 10183 (36), 15409 (4); Griffiths 94 (15), 107 (28), 4836 (28), 4976 (28), 7032 (15); Griscom 16409 (4); Guerrero 632 (36); Gutte 185 (36).

Hall 764 (4); Harkins 809 (4); Harvey 1038 (3), 1458 (15), 1764 (4), 1854 (4); Havard 26 (15), s.n. (15); Henderson 91–03 (4), 94–29 (4); Henrickson 15143 a (15), 15226 (15); Hermann 3201 (4), 4198 (4); Hernandez Xolocotzi X-2443 (15), X-2828 (36), X-2836 (36); Hill 14632 (15); Hinckley 245 (28), 493 (28); Hinton 1336 (36), 1893 (36), 2315 (36), 2316 (36); Hitchcock 520 (4), 812 (5), 813 (28), 837 (15), 967 (5), 1271 (4), 1318 (4), 1341 (4), 1346 (4), 1903 (28), 3715 (15), 3776 (15), 5947 (36), 5965 (36), 5973 (36), 6019 (36), 6266 (36), 6733 (8), 7151 (36), 7169 (36), 7677 (28), 7681 (28), 7741 (15), 12616 (4), 13511 (15), 13553 (28), s.n. (4); Hoffmann s.n. (4); Hoge 260 (15); Hoogstraal 991 (36); House 2101 (4).

Iltis 213 (15), 214 (8), 958 (31), 23032 (4); Innes 1130 (15).

Jacob 815 (4); Jones 479 (36), 24157 (4).

Kearney 10114 (15), 10541 (28); Kearney Jr. 1102 (4); Kellogg 82 (4); King 3378 (31), 5132 (36), 5151 (36); Kneucker 564 (4); Knieskern s.n. (4); Koch 762 (36), 75709 (36), 77110 (15); Kral 2065 (4), 25586 (15), 34987 (4), 42587 (4), 45353 (4), 45934 (4), 46012 (4), 46479 (4), 55030 (4); Krauch 6495 (15).

Larrick 249 (4); Latham 2755 (4), 4087 (4), 22391 (4); Le Doux 2086 (31); Le Sueur 143 (15); Leavenworth 1077 (36); Lemmon 2923 (15), 4678 (28); Liberman 1110 (26); Longhi-Wagner 2121 (1), 2497 (1); Lundell 13153 (15); Luz 39 (26), Lyonnet 48 (15), 62 a (36), 1826 (36), 1877 (36), 1948 (31), 2498 (36), 2511 (31), 2512 (31), 2527 (36), 2684 (36), 2719 (31).

Mackenzie 3109 (4); Madrigal A. s.n. (15); Manzanero M. 450 (36); Marsh Jr. 629 (28); Martínez 1063 (31); Matthews s.n. (4); Matuda 18907 (36), 19202 (31), 21268 (36), 21645 (36), 25724 (36), 25753 (36), 25755 (36), 25777 (36), 29473 (36), 29776 (3), 31875 (36); McCarthy s.n. (4); McDaniel 1811 (4); McDougall 1818 (4); McGregor 57 (15), 406 (15); McVaugh 12268 (36); Mearns 2573 (28); Meislahn 191 (5); Mejía S. 218 (31); Mendoza 2640 (15); Metcalfe 746 (15); Metzler 2 (36); Mez 3164 (15), 3166 (15); Mick 87 (8), 180 (31), 287 (15), 305 (36); Miller Jr. s.n. (4); Mohr s.n. (4); Moore 3172 (15), 3605 (15), 4164 (15); Moore Jr. 1233 (31), 2843 (36), 5583 (36); Moorgen s.n. (29); Morong s.n. (4); Mueller 2342 (15), 2442 (15), 7948 a (15); Mujica Sallés 2 (20), 22 (28), 42 (26), 46 (26), 47 (26), 63 (33 a), 72 (26), 74 A (26), 81 (20), 83 (29), 130 (35), 141 (22), 142 (22), 144 (35), 151 (20), 155 (22), 166 (26).

Nealley s.n. (4); Neally 129 (15); Nee 22928 (36), 24775 (31); Nelson 1373 (36), 1373a (31); Noyes s.n. (4).

O'Neill 491 (4); Ortiz 1132 (36), 1194 (36).

Palmer 339 (15), 5154 (4), 5248 (4), 24541 (4), 31887 (15); Pedersen 5188 (35), 13333 (24); Peebles 3389 (15); Pennell 17704 (15), 8929 (28), 18940 (15); Peterson 4010 (15); Piedmont 4311 (4); Plank 53 (4); Pringle 18 (28), 502 (15), 639 (15), 3035 (15), 4759 (36), 5200 (31), 6236 (36), 6588 (36), 7606 (8), 8595 (15), 9574 (36), 13249 (31), s.n. (15); Purpus 3589 (15).

Quarín 3163 (33a).

Redfield 4317 (4); Reeder 233 (4), 2221 (31), 3295 (15); Renvoize 3025 (20), 4143 (23); Reverchon 4128 (4), s.n. (4); Rivero 1384 (23); Robinson 1 (4); Rodriguez 1284 (31); Roivainen 481 (11); Rolfe 43 (4); Rose 2750 (36), 5671 (36), 8680 (8), 8700 (36), 8744 (15); Rugel 1849 (4), s.n. (4); Rúgolo 1611 (23); Ruiz 326 (15); Ruth 93 (4), s.n. (4); Rzedowski 623 (36), 11940 (31), 16904 (15), 17547 (15), 17704 (15), 35555 (31), 35863 (8), 50768 (8).

Sánchez Vega 2458 (34), 2769 (34), 2935 (30), 4984 (30); Sánchez-Ken 141 (15); Sandoval 68 (31); Schaack 2881 (4); Schinini 19229 (35); Schultz 41 (4), 14705 (23); Scribner 138 (4), 266 (4); Scully 652 (4); Serrato Sánchez s.n. (15); Seymour 109 (4), 1060 (4); Sharp 44144 (31), s.n. (4); Shinners 7029 (4); Shreve 7707 (15); Silveus 727 (15), 785 (15), 3470 (28); Simpson s.n. (4); Smith 926 (36), 3327 (18), 8302 (14), 10109 B (18), 10331 (26), 10488 (18), 10960 (34), 10964 (18), 11038 (18), 11794 A (18); Snow 6721 (31); Soderstrom 141 (28), 493 (36), 752 (15); Sohns 177 (36), 289 (15), 300 (15), 424 (15), 505 (15), 507 (15), 533 (15), 534 (15), 538 (36), 553 (8),

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36. *Piptochaetium virescens* (Kunth) Parodi

Aleman 267 (26); Alonso J. 151 (20); Andrews s.n. (4); Arriaga C. 351 (31); Arzivenco 349 (20), 352 (28).

Baker 115 (5), 1155 (5); Banda 132 (8); Barclay 8455 (34); Barkley 14 A 660 (15); Bartlett 10225 (33a); Bartley 2011 (4); Beaman 3928 (31), 4155 (31), 4273 (31), 4329 (31), 4387 (36); Beetle M-141 (36), M-4743 (36), M-7086 (36), M-7338 (15), M-7742 (15), M-7856 (28), M-7864 (15); Berkley 1579 (4); Biswell 94408 (4); Boechat 160 (28), 161 (20); Bonner 354 (4); Boott s.n. (4); Boufford 18242 (4); Bozeman 8842 (4); Brandegee 31 (15), 34 (15); Brant 2239 (15); Braun 1422 (4), 942 (4); Breedlove 14171 (36), 39241 (36), 43293 (15), 44133 (15); Bro. Arsène 2699 (36), 5305 (36), 5375 (36), 6749 (36); Brunken 234 (15), 247 (36), 387 (36); Burgess 227 (4).

Calzada 4645 (15); Carter 2396 (15); Castillo 1980 (31); Chapman 1037 (4); Chase 7220 (4), 7312 (4), 7401 (4); Chazaro 3792 (31); Chiang 9077 (15); Chimal 9 (36), 1954 (31); Churchill 123 (4), s.n. (4); Cole s.n. (4); Collins s.n. (4); Combo 876 (4); Commons 269 (4); Correll 353 (4), 13699 (15), 16170 (4); Cronquist 4311 (4), 4432 (4), 5014 (4), 5075 (4); Curtiss 5834 (5).

Darrow 1287 (15); Davidse 9287 (15), 9485 (15), 9832 (36), 10031 (15), 11137 A (33a), 29775 (15); De Chalmot s.n. (4); De Koninck 73 (36), 114 (31); Deam 20709 (4), 36302 (4), 40704 (4), 64413 (4); Demaree 14586 (4), 19003 (4), 63483 (4); Dowell 7309 (5); Duncan 9485 (4); Durán E. 498 (31).

Earle 165 (15); Early s.n. (4); Eggert 36 (4), s.n. (4); Egler 41–136 (4); Ellis 1113 (31); Escobedo 1478 (31).

Faircloth 5079 (4), 5798 (4), 7070 (4); Felger 92–794 (15); Fernald 7760 (4); Fernández 734 (28), 735 (20); Ferris 2736 (15), 2812 (15); Fisher 108 (31), s.n. (31), s.n. (4); Fogg Jr. 2224 (4); Fredholm 5092 (5), 5725 (5); Freeman 54117 (4).

Garber s.n. (4); Gentry 8492 (15); Gleason 8537 (4); Godfrey 3686 (4), 8085 (4), 67795 (4); Gould 2456 (28), 3768 (28), 4419 (15), 9211 (8), 9602 (15), 9661 (15), 10183 (36), 15409 (4); Griffiths 94 (15), 107 (28), 4836 (28), 4976 (28), 7032 (15); Griscom 16409 (4); Guerrero 632 (36); Gutte 185 (36).

Hall 764 (4); Harkins 809 (4); Harvey 1038 (3), 1458 (15), 1764 (4), 1854 (4); Havard 26 (15), s.n. (15); Henderson 91–03 (4), 94–29 (4); Henrickson 15143 a (15), 15226 (15); Hermann 3201 (4), 4198 (4); Hernandez Xolocotzi X-2443 (15), X-2828 (36), X-2836 (36); Hill 14632 (15); Hinckley 245 (28), 493 (28); Hinton 1336 (36), 1893 (36), 2315 (36), 2316 (36); Hitchcock 520 (4), 812 (5), 813 (28), 837 (15), 967 (5), 1271 (4), 1318 (4), 1341 (4), 1346 (4), 1903 (28), 3715 (15), 3776 (15), 5947 (36), 5965 (36), 5973 (36), 6019 (36), 6266 (36), 6733 (8), 7151 (36), 7169 (36), 7677 (28), 7681 (28), 7741 (15), 12616 (4), 13511 (15), 13553 (28), s.n. (4); Hoffmann s.n. (4); Hoge 260 (15); Hoogstraal 991 (36); House 2101 (4).

Iltis 213 (15), 214 (8), 958 (31), 23032 (4); Innes 1130 (15).

Jacob 815 (4); Jones 479 (36), 24157 (4).

Kearney 10114 (15), 10541 (28); Kearney Jr. 1102 (4); Kellogg 82 (4); King 3378 (31), 5132 (36), 5151 (36); Kneucker 564 (4); Knieskern s.n. (4); Koch 762 (36), 75709 (36), 77110 (15); Kral 2065 (4), 25586 (15), 34987 (4), 42587 (4), 45353 (4), 45934 (4), 46012 (4), 46479 (4), 55030 (4); Krauch 6495 (15).

Larrick 249 (4); Latham 2755 (4), 4087 (4), 22391 (4); Le Doux 2086 (31); Le Sueur 143 (15); Leavenworth 1077 (36); Lemmon 2923 (15), 4678 (28); Liberman 1110 (26); Longhi-Wagner 2121 (1), 2497 (1); Lundell 13153 (15); Luz 39 (26), Lyonnet 48 (15), 62 a (36), 1826 (36), 1877 (36), 1948 (31), 2498 (36), 2511 (31), 2512 (31), 2527 (36), 2684 (36), 2719 (31).

Mackenzie 3109 (4); Madrigal A. s.n. (15); Manzanero M. 450 (36); Marsh Jr. 629 (28); Martínez 1063 (31); Matthews s.n. (4); Matuda 18907 (36), 19202 (31), 21268 (36), 21645 (36), 25724 (36), 25753 (36), 25755 (36), 25777 (36), 29473 (36), 29776 (3), 31875 (36); McCarthy s.n. (4); McDaniel 1811 (4); McDougall 1818 (4); McGregor 57 (15), 406 (15); McVaugh 12268 (36); Mearns 2573 (28); Meislahn 191 (5); Mejía S. 218 (31); Mendoza 2640 (15); Metcalfe 746 (15); Metzler 2 (36); Mez 3164 (15), 3166 (15); Mick 87 (8), 180 (31), 287 (15), 305 (36); Miller Jr. s.n. (4); Mohr s.n. (4); Moore 3172 (15), 3605 (15), 4164 (15); Moore Jr. 1233 (31), 2843 (36), 5583 (36); Moorgen s.n. (29); Morong s.n. (4); Mueller 2342 (15), 2442 (15), 7948 a (15); Mujica Sallés 2 (20), 22 (28), 42 (26), 46 (26), 47 (26), 63 (33 a), 72 (26), 74 A (26), 81 (20), 83 (29), 130 (35), 141 (22), 142 (22), 144 (35), 151 (20), 155 (22), 166 (26).

Nealley s.n. (4); Neally 129 (15); Nee 22928 (36), 24775 (31); Nelson 1373 (36), 1373a (31); Noyes s.n. (4).

O'Neill 491 (4); Ortiz 1132 (36), 1194 (36).

Palmer 339 (15), 5154 (4), 5248 (4), 24541 (4), 31887 (15); Pedersen 5188 (35), 13333 (24); Peebles 3389 (15); Pennell 17704 (15), 8929 (28), 18940 (15); Peterson 4010 (15); Piedmont 4311 (4); Plank 53 (4); Pringle 18 (28), 502 (15), 639 (15), 3035 (15), 4759 (36), 5200 (31), 6236 (36), 6588 (36), 7606 (8), 8595 (15), 9574 (36), 13249 (31), s.n. (15); Purpus 3589 (15).

Quarín 3163 (33a).

Redfield 4317 (4); Reeder 233 (4), 2221 (31), 3295 (15); Renvoize 3025 (20), 4143 (23); Reverchon 4128 (4), s.n. (4); Rivero 1384 (23); Robinson 1 (4); Rodriguez 1284 (31); Roivainen 481 (11); Rolfe 43 (4); Rose 2750 (36), 5671 (36), 8680 (8), 8700 (36), 8744 (15); Rugel 1849 (4), s.n. (4); Rúgolo 1611 (23); Ruiz 326 (15); Ruth 93 (4), s.n. (4); Rzedowski 623 (36), 11940 (31), 16904 (15), 17547 (15), 17704 (15), 35555 (31), 35863 (8), 50768 (8).

Sánchez Vega 2458 (34), 2769 (34), 2935 (30), 4984 (30); Sánchez-Ken 141 (15); Sandoval 68 (31); Schaack 2881 (4); Schinini 19229 (35); Schultz 41 (4), 14705 (23); Scribner 138 (4), 266 (4); Scully 652 (4); Serrato Sánchez s.n. (15); Seymour 109 (4), 1060 (4); Sharp 44144 (31), s.n. (4); Shinners 7029 (4); Shreve 7707 (15); Silveus 727 (15), 785 (15), 3470 (28); Simpson s.n. (4); Smith 926 (36), 3327 (18), 8302 (14), 10109 B (18), 10331 (26), 10488 (18), 10960 (34), 10964 (18), 11038 (18), 11794 A (18); Snow 6721 (31); Soderstrom 141 (28), 493 (36), 752 (15); Sohns 177 (36), 289 (15), 300 (15), 424 (15), 505 (15), 507 (15), 533 (15), 534 (15), 538 (36), 553 (8), 581 (15), 601 (36), 603 (36), 604 (31), 782 (15), 790 (36), 799 (36), 804 (36), 819 (36), 977 (36), 982 (36), 1012 (31), 1016 (31), 1022 (15), 1064 (15), 1147 (15), 1500 (36), 1535 (8); Solomon 1535 (4), 1710 (4), 11342 (23); Sperry 370 (15); St. Pierre 888 (36); Standley 40512 (15), 40699 (15), s.n. (15); Stanford 2482 (4), 2604 (15); Steyermark 3172 (15), 36700 (36), 48274 (31), 48452 (31), 50955 (36); Strong 1342 (4); Svenson 10246 (4); Swallen 951 (4), 1109 (15), 7561 (35).

Talbot 8 (4); Taylor 276 (15), 6254 (15); Tenorio 1197 (15); Tharp 4175 (28); Thieret 19497 (4), 22502 (4), 28558 (4); Thorne 2592 (4), 3348 (4); Toolin 2222 (15); Torres 875 (36), 1226 (29); Tracy 130 (28), 4544 (4), 7031 (5), s.n. (4); Traylor 61 (31); Tuckerman 848 (4).

Valencia 442 (22), s.n. (23); Valls 1233 (20), 2215 (20), 2805 (20), 2821 (33 a), 2931 (20), 2939 (33 a), 12188 (22), 12259 (35); Van Eseltime 127 (4); Van Schaack 3575 (4); Van Sickle s.n. (4); Vasey s.n. (4); Velazco Torres s.n. (31); Ventura A. 376 (36), 2153 (15), 18506 (31); Vera Santos 24 (15), 1921 (15), 1922 (28), 1959 (28), 2155 (15); Villarreal 1975 (28).

Warner s.n. (4); Warnock 12082 (28), 46717 (15); Warnock T 598 (15); Waterfall 6322 (15), 12627 (15), 14854 (4), 16410 (36); Weatherby 4122 (4), 5831 (4), 6234 (4); Weatherways 16 (4), 37 (4); West 26673 (4); Whiting 811 (15), 887 (15); Wilcox s.n. (15); Wolff 4974 (4); Wooton s.n. (15); Wynd 643 (15).

Yacolucci 843 (4).

Zanin s.n. (1), 18 (1); Zavala Ch. 245 (31), 862 (15); Zöllner 8672 (32).

Appendix 2

Specimens of *Hesperostipa* and *Nassella* used for morphological and cladistic analyses, as outgroups of *Piptochaetium.*

Hesperostipa comata (Trinius & Ruprecht) Barkworth (= *Stipa comata* Trin. & Rupr.).

U.S.A. **Colorado:** El Paso Co., *Ehlers 7526* (UTC). **Nevada:** Elko Co., E side of Ruby Mtns., 0.7 road mi. S of Shantytown, *Williams et al. 84–49–8* (UTC). **Utah:** Garfield Co., located at the head of South Fork, Dugout Creek on the North Mountain in the Henry Mountains, *Nelson s.n.* (UTC 101953).

Hesperostipa neomexicana (Thurber) Barkworth (= *Stipa pennata* L. var. *neomexicana* Thurber).

U.S.A. **Arizona:** without locality, *Williams 3051* (BAA). **Texas:** San Antonio, *Silveus 1215* (BAA).

Hesperostipa spartea (Trinius) Barkworth (= *Stipa spartea* Trin.).

U.S.A. **Colorado:** Bookvale, Clear Creek Co., *Churchill s.n.* (BAA 15155). **Illinois:** Stark Co., Wady Petra, *Chase 808* (BAA). **Indiana:** Pulaski Co., sandy soil along Pennsylvania railroad and hwy. 29, 2.3 mi. S of Winamac, *Potzger 4243* (BAA).

Nassella charruana (Arechavaleta) Barkworth (= *Stipa charruana* Arechav.).

ARGENTINA. **Entre Ríos:** Gualeguaychú, *Burkart 25865* (SI); Gualeguaychú, ruta 12, km 180, *Burkart & Crespo 22895* (SI).

Nassella leucotricha (Trinius & Ruprecht) R. W. Pohl (= *Stipa leucotricha* Trin. & Rupr.).

MEXICO. **Coahuila:** Arteaga, Sierra de Arteaga, cañón de Jame, 5 mi. E de Jame, *Hoge 249* (UTC). U.S.A. **California:** Sonoma Co., near Sonoma, *Heller 5350* (SI). **Texas:** Bee Co., *Herb. Univ. Texas 2154* (SI); Karnes Co., roadside shoulder immediately S of Karnes City, *Isely 10634* (UTC).

Nassella meyeniana (Trinius & Ruprecht) Parodi (= *Urachne meyeniana* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Cochinoca, Abra Pampa, *Venturi 9385* (SI). **Humahuaca:** Tres Cruces, *Parodi 9609* (SI); Sierra del Aguila, *Venturi 8726* (SI).

Nassella pubiflora (Trinius & Ruprecht) E. Desvaux (= *Urachne pubiflora* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Humahuaca, camino a Palca de Aparzo, *Kiesling & López 3624* (SI). **Tucumán:** Tafí, km 82, Quebrada del Barón, *Diers 282* (SI).

Nassella pulchra (Hitchcock) Barkworth (= *Stipa pulchra* Hitchc.).

U.S.A. **California:** Marin Co., 5 mi. W of Mill Valley, *Beetle 2722* (SI); Contra Costa Co., Orinda, in sandy soil of open cut, *Beetle 1718* (SI); Marin Co., San Rafael Hills, *Howell 16251* (UTC).

Nassella pungens E. Desvaux

CHILE. **IV Región:** Coquimbo, *Yiles 472* (SI).

Nassella tenuissima (Trinius) Barkworth (= *Stipa tenuissima* Trin.).

MEXICO. **Veracruz:** between Tziutlán and Perote, *Beetle M-581* (UTC). ARGENTINA. **Córdoba:** Ea. San Teodoro, *Stuckert 198* (SI). **La Pampa:** Toay, Ea. Anquiló, *Rúgolo 1060* (SI). **Tucumán:** Tafí del Valle, *Hueck 9* (SI).

Nassella trichotoma (Nees) Hackel ex Arechavaleta (= *Stipa trichotoma* Nees).

ARGENTINA. **Buenos Aires:** Bolívar, Pirovano, *Burkart 7076* (SI); Tandil, *Troncoso 1290* (SI). **Entre Ríos:** E. Carbó, orillas de vías férreas, *Burkart 18129* (SI).

Appendix 3

List of characters and character states. A description of the characters and character states and their range of variation are presented as considered in the cladistic analysis.

1. Lemma margins: not involute = 0; involute = 1.
2. Palea shape: flat on abaxial surface = 0; bikeeled on the abaxial surface = 1.
3. Palea length: half the length of the lemma to equal the length of the lemma = 0; longer than the lemma = 1; shorter than half the length of the lemma = 2 (Fig. 2A, B).
4. Palea venation: nerveless = 0; 2-nerved = 1.
5. Long fundamental cells of the lemma epidermis: absent = 0; present = 1.
6. Fundamental cell sidewalls: irregularly sinuate = 0; regularly dentate = 1; regularly sinuate = 2. Epidermal characters (5, 6), were taken from Thomasson (1978a), Barkworth (1990), and Torres (1997).
7. Callus length: shorter than 0.8 mm = 0; equal to or longer than 0.8 mm = 1. Callus length is variable within *Piptochaetium*; it is usually long in species with cylindrical or obconical florets but short in obovoid or lens-shaped florets. In *Nassella* the callus is variable in length, while it is always long in *Hesperostipa.*
8. Callus shape: acute or subacute = 0 (Fig. 5A–E); blunt or truncate = 1 (Fig. 5F–H). The callus, when short, is generally truncate or blunt; if long, it is acute or subacute. Callus shape varies also within *Nassella* s.l., while in *Hesperostipa* it is always acute. Charac-

581 (15), 601 (36), 603 (36), 604 (31), 782 (15), 790 (36), 799 (36), 804 (36), 819 (36), 977 (36), 982 (36), 1012 (31), 1016 (31), 1022 (15), 1064 (15), 1147 (15), 1500 (36), 1535 (8); Solomon 1535 (4), 1710 (4), 11342 (23); Sperry 370 (15); St. Pierre 888 (36); Standley 40512 (15), 40699 (15), s.n. (15); Stanford 2482 (4), 2604 (15); Steyermark 3172 (15), 36700 (36), 48274 (31), 48452 (31), 50955 (36); Strong 1342 (4); Svenson 10246 (4); Swallen 951 (4), 1109 (15), 7561 (35).

Talbot 8 (4); Taylor 276 (15), 6254 (15); Tenorio 1197 (15); Tharp 4175 (28); Thieret 19497 (4), 22502 (4), 28558 (4); Thorne 2592 (4), 3348 (4); Toolin 2222 (15); Torres 875 (36), 1226 (29); Tracy 130 (28), 4544 (4), 7031 (5), s.n. (4); Traylor 61 (31); Tuckerman 848 (4).

Valencia 442 (22), s.n. (23); Valls 1233 (20), 2215 (20), 2805 (20), 2821 (33 a), 2931 (20), 2939 (33 a), 12188 (22), 12259 (35); Van Eseltime 127 (4); Van Schaack 3575 (4); Van Sickle s.n. (4); Vasey s.n. (4); Velazco Torres s.n. (31); Ventura A. 376 (36), 2153 (15), 18506 (31); Vera Santos 24 (15), 1921 (15), 1922 (28), 1959 (28), 2155 (15); Villarreal 1975 (28).

Warner s.n. (4); Warnock 12082 (28), 46717 (15); Warnock T 598 (15); Waterfall 6322 (15), 12627 (15), 14854 (4), 16410 (36); Weatherby 4122 (4), 5831 (4), 6234 (4); Weatherways 16 (4), 37 (4); West 26673 (4); Whiting 811 (15), 887 (15); Wilcox s.n. (15); Wolff 4974 (4); Wooton s.n. (15); Wynd 643 (15).

Yacolucci 843 (4).

Zanin s.n. (1), 18 (1); Zavala Ch. 245 (31), 862 (15); Zöllner 8672 (32).

Appendix 2

Specimens of *Hesperostipa* and *Nassella* used for morphological and cladistic analyses, as outgroups of *Piptochaetium*.

Hesperostipa comata (Trinius & Ruprecht) Barkworth (= *Stipa comata* Trin. & Rupr.).

U.S.A. **Colorado:** El Paso Co., *Ehlers 7526* (UTC). **Nevada:** Elko Co., E side of Ruby Mtns., 0.7 road mi. S of Shantytown, *Williams et al. 84–49–8* (UTC). **Utah:** Garfield Co., located at the head of South Fork, Dugout Creek on the North Mountain in the Henry Mountains, *Nelson s.n.* (UTC 101953).

Hesperostipa neomexicana (Thurber) Barkworth (= *Stipa pennata* L. var. *neomexicana* Thurber).

U.S.A. **Arizona:** without locality, *Williams 3051* (BAA). **Texas:** San Antonio, *Silveus 1215* (BAA).

Hesperostipa spartea (Trinius) Barkworth (= *Stipa spartea* Trin.).

U.S.A. **Colorado:** Bookvale, Clear Creek Co., *Churchill s.n.* (BAA 15155). **Illinois:** Stark Co., Wady Petra, *Chase 808* (BAA). **Indiana:** Pulaski Co., sandy soil along Pennsylvania railroad and hwy. 29, 2.3 mi. S of Winamac, *Potzger 4243* (BAA).

Nassella charruana (Arechavaleta) Barkworth (= *Stipa charruana* Arechav.).

ARGENTINA. **Entre Ríos:** Gualeguaychú, *Burkart 25865* (SI); Gualeguaychú, ruta 12, km 180, *Burkart & Crespo 22895* (SI).

Nassella leucotricha (Trinius & Ruprecht) R. W. Pohl (= *Stipa leucotricha* Trin. & Rupr.).

MEXICO. **Coahuila:** Arteaga, Sierra de Arteaga, cañón de Jame, 5 mi. E de Jame, *Hoge 249* (UTC). U.S.A. **California:** Sonoma Co., near Sonoma, *Heller 5350* (SI). **Texas:** Bee Co., *Herb. Univ. Texas 2154* (SI); Karnes Co., roadside shoulder immediately S of Karnes City, *Isely 10634* (UTC).

Nassella meyeniana (Trinius & Ruprecht) Parodi (= *Urachne meyeniana* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Cochinoca, Abra Pampa, *Venturi 9385* (SI). **Humahuaca:** Tres Cruces, *Parodi 9609* (SI); Sierra del Aguila, *Venturi 8726* (SI).

Nassella pubiflora (Trinius & Ruprecht) E. Desvaux (= *Urachne pubiflora* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Humahuaca, camino a Palca de Aparzo, *Kiesling & López 3624* (SI). **Tucumán:** Tafí, km 82, Quebrada del Barón, *Diers 282* (SI).

Nassella pulchra (Hitchcock) Barkworth (= *Stipa pulchra* Hitchc.).

U.S.A. **California:** Marin Co., 5 mi. W of Mill Valley, *Beetle 2722* (SI); Contra Costa Co., Orinda, in sandy soil of open cut, *Beetle 1718* (SI); Marin Co., San Rafael Hills, *Howell 16251* (UTC).

Nassella pungens E. Desvaux

CHILE. **IV Región:** Coquimbo, *Yiles 472* (SI).

Nassella tenuissima (Trinius) Barkworth (= *Stipa tenuissima* Trin.).

MEXICO. **Veracruz:** between Tziutlán and Perote, *Beetle M-581* (UTC). ARGENTINA. **Córdoba:** Ea. San Teodoro, *Stuckert 198* (SI). **La Pampa:** Toay, Ea. Anquiló, *Rúgolo 1060* (SI). **Tucumán:** Tafí del Valle, *Hueck 9* (SI).

Nassella trichotoma (Nees) Hackel ex Arechavaleta (= *Stipa trichotoma* Nees).

ARGENTINA. **Buenos Aires:** Bolívar, Pirovano, *Burkart 7076* (SI); Tandil, *Troncoso 1290* (SI). **Entre Ríos:** E. Carbó, orillas de vías férreas, *Burkart 18129* (SI).

Appendix 3

List of characters and character states. A description of the characters and character states and their range of variation are presented as considered in the cladistic analysis.

1. Lemma margins: not involute = 0; involute = 1.
2. Palea shape: flat on abaxial surface = 0; bikeeled on the abaxial surface = 1.
3. Palea length: half the length of the lemma to equal the length of the lemma = 0; longer than the lemma = 1; shorter than half the length of the lemma = 2 (Fig. 2A, B).
4. Palea venation: nerveless = 0; 2-nerved = 1.
5. Long fundamental cells of the lemma epidermis: absent = 0; present = 1.
6. Fundamental cell sidewalls: irregularly sinuate = 0; regularly dentate = 1; regularly sinuate = 2. Epidermal characters (5, 6), were taken from Thomasson (1978a), Barkworth (1990), and Torres (1997).
7. Callus length: shorter than 0.8 mm = 0; equal to or longer than 0.8 mm = 1. Callus length is variable within *Piptochaetium*; it is usually long in species with cylindrical or obconical florets but short in obovoid or lens-shaped florets. In *Nassella* the callus is variable in length, while it is always long in *Hesperostipa*.
8. Callus shape: acute or subacute = 0 (Fig. 5A–E); blunt or truncate = 1 (Fig. 5F–H). The callus, when short, is generally truncate or blunt; if long, it is acute or subacute. Callus shape varies also within *Nassella* s.l., while in *Hesperostipa* it is always acute. Charac-

ters 7 and 8 were traditionally considered as diagnostic to identify *Piptochaetium* sects. *Podopogon* and *Piptochaetium* (Parodi, 1944; Sánchez Vega, 1991; Cialdella & Arriaga, 1998). *Piptochaetium* sect. *Podopogon* generally included species with a long and acute or subacute callus, while *Piptochaetium* sect. *Piptochaetium* presented species with a short and blunt callus.

9. Callus pubescence: glabrous or slightly hairy = 0; densely hairy = 1. Most *Piptochaetium* species have florets with a densely pubescent callus (Fig. 5A–G). It is usually glabrous or only slightly pubescent in *Piptochaetium brevicalyx* (Fig. 5H), *P. calvescens*, *P. cucullatum*, *P. hirtum*, *P. lejopodum*, *P. montevidense*, *P. panicoides*, and *P. tovarii*. In *Nassella* the callus is glabrous or pubescent, with trichomes densely to slightly disposed, while in *Hesperostipa* the callus is always densely pubescent.
10. Awn: persistent = 0; deciduous = 1.
11. Inflorescence branches: densely flowered = 0; not densely flowered = 1. This character varies among species of *Piptochaetium* and *Nassella*, in which the branches may be densely or loosely flowered, while in *Hesperostipa* branches are loosely flowered.
12. Upper glume length: longer than the floret = 0; equal to the floret = 1. Species of *Piptochaetium*, *Nassella*, and *Hesperostipa* have upper glumes longer than the floret. Only in *P. alpinum* and *P. brevicalyx* is the upper glume as long as the floret.
13. Floret shape: terete to fusiform = 0 (Fig. 5A–G); obconical = 1 (Cialdella & Arriaga, 1998, fig. 8B, D); obovoid to globose = 2 (Fig. 5H); lens-shaped = 3 (Cialdella & Arriaga, 1998: fig. 10C, D). Floret shape varies among species of *Piptochaetium*, being terete, fusiform, obconical, obovoid, or lens-shaped. *Nassella* presents terete, obovoid, or lens-shaped florets, while in *Hesperostipa* florets are always terete.
14. Lateral compression of the floret: absent or slightly compressed = 0 (Fig. 5A–H); conspicuously compressed = 1 (Cialdella & Arriaga, 1998: figs. 9C, 10C, D). This character is variable among species of *Piptochaetium* and *Nassella*, while in *Hesperostipa* the florets are never laterally compressed.
15. Lemma pubescence: absent = 0 (Figs. 1A, 5H); present = 1 (Figs. 1B, 5G).
16. Papillae of the lemma: absent = 0; present = 1 (Cialdella & Arriaga, 1998: figs. 2D, 10C). Papillae are found in a few species within *Piptochaetium* and *Nassella*, but are always absent in *Hesperostipa*.
17. Prickles of the lemma: absent = 0; present = 1 (Fig. 1C, D).
18. Prickles over almost all the lemma surface: absent = 0; present = 1 (Fig. 2D).
19. Prickles on the distal third of the lemma: absent = 0; present = 1 (Figs. 2C, 5A, B). Hooks are similar to prickles, although these appendages differ slightly (Ellis, 1979). These characters were recognized as homologous by Metcalfe (1960). Intermediate forms can also be found, making it a difficult character to classify. In addition, the presence and distribution of hooks and prickles are similar in all the species analyzed. These epidermal appendages are found in some species of *Piptochaetium*, *Nassella*, and all species of *Hesperostipa*. Distribution of prickles (characters 18, 19) varies among species, although it is always constant within species. Only the distribution of appendages in *P. stipoides* var. *stipoides* (Cialdella & Arriaga, 1998: fig. 10F–I) is highly variable, even within a specimen.
20. Base of prickles: surrounded but not covered by adjacent epidermal cells = 0; partially covered by adjacent epidermal cells = 1 (Cialdella & Arriaga, 1998: fig. 3D). Partially covered prickle bases occur only in *Piptochaetium stipoides* var. *echinulatum* Parodi.
21. Lemma width just below the crown: as wide as the crown = 0; narrower than the crown = 1. This character is related to floret shape: lemmas of cylindrical florets are usually as wide as the crown or slightly narrowed, while in obconical, obovoid, and lens-shaped florets lemmas are conspicuously narrowed below the crown, being more conspicuous in gibbous florets.
22. Crown contracted to the base of the awn: absent = 0; present = 1 (Fig. 5). The crown concept was discussed by different authors (Spegazzini, 1901; Parodi, 1944; Barkworth, 1990; Muñoz-Schick, 1990; Jacobs et al., 1995; Cialdella & Arriaga, 1998). As interpreted here, it refers to the distal portion of the lemma, which is fused to the base of the awn (Barkworth, 1990; Cialdella & Arriaga, 1998). In *Piptochaetium* the crown can be contracted or not; when not contracted, it exceeds the diameter of the awn (Cialdella & Arriaga, 1998: figs. 9E, 10B). *Nassella* and *Hesperostipa* present a contracted crown, being membranous, loose, parted, and, in some species of *Nassella*, sheathing at the base of the awn (Barkworth, 1990).
23. Crown shape: straight, not revolute = 0 (Cialdella & Arriaga, 1998: fig. 10E); revolute toward the outside = 1 (Cialdella & Arriaga, 1998: fig. 9E). Some species of *Piptochaetium* show a revolute crown like a ring, generally covered by prickles, hooks, and sometimes macrohairs. In *Nassella* and *Hesperostipa* the crown is always straight.
24. Macrohairs in the crown: absent = 0 (Fig. 2A); present = 1 (Fig. 2C). This character is only variable in *P. stipoides* var. *stipoides* and *P. fimbriatum*. These appendages are frequently associated with other types of epidermal appendages such as prickles and hooks.
25. Papillae in the crown: absent = 0; present = 1 (Cialdella & Arriaga, 1998: fig. 3C). These appendages are found in a few species of *Piptochaetium*, while they are absent in *Nassella* and *Hesperostipa*.
26. Prickles in the crown: absent = 0 (Fig. 2A); present = 1 (Fig. 2C, D). This type of epidermal appendage is frequent in several species of *Piptochaetium* and *Nassella*, and completely absent in a few species; in *Hesperostipa* it is always present.
27. Awn shape: thread-like = 0 (Fig. 5H); cone-shaped = 1 (Cialdella & Arriaga, 1998: fig. 9F). In *Nassella*, *Hesperostipa*, and almost all species of *Piptochaetium*, the awn is thread-like, bigeniculate, shortly hispid, and twisted in its basal portion. Only in *Piptochaetium cucullatum* is the awn cone-shaped, right or slightly curved but not twisted, its base as wide as the crown (0.9–1 mm wide).
28. Floret length/width ratio: > 3.6 = 0; < 3.5 = 1.
29. Crown width: narrow [0.4–0.6(–0.9) mm diam.] = 0; wide (1–1.8 mm diam.) = 1. In *Piptochaetium*, the crown is narrow when contracted to the base of the awn, except in *Piptochaetium cucullatum*, which presents a wide and contracted crown (Cialdella & Arriaga, 1998: fig. 9F) due to the conical shape of the awn. In *Nassella* and *Hesperostipa* the crown is always narrow in shape.

ters 7 and 8 were traditionally considered as diagnostic to identify *Piptochaetium* sects. *Podopogon* and *Piptochaetium* (Parodi, 1944; Sánchez Vega, 1991; Cialdella & Arriaga, 1998). *Piptochaetium* sect. *Podopogon* generally included species with a long and acute or subacute callus, while *Piptochaetium* sect. *Piptochaetium* presented species with a short and blunt callus.

9. Callus pubescence: glabrous or slightly hairy = 0; densely hairy = 1. Most *Piptochaetium* species have florets with a densely pubescent callus (Fig. 5A–G). It is usually glabrous or only slightly pubescent in *Piptochaetium brevicalyx* (Fig. 5H), *P. calvescens*, *P. cucullatum*, *P. hirtum*, *P. lejopodum*, *P. montevidense*, *P. panicoides*, and *P. tovarii*. In *Nassella* the callus is glabrous or pubescent, with trichomes densely to slightly disposed, while in *Hesperostipa* the callus is always densely pubescent.
10. Awn: persistent = 0; deciduous = 1.
11. Inflorescence branches: densely flowered = 0; not densely flowered = 1. This character varies among species of *Piptochaetium* and *Nassella*, in which the branches may be densely or loosely flowered, while in *Hesperostipa* branches are loosely flowered.
12. Upper glume length: longer than the floret = 0; equal to the floret = 1. Species of *Piptochaetium*, *Nassella*, and *Hesperostipa* have upper glumes longer than the floret. Only in *P. alpinum* and *P. brevicalyx* is the upper glume as long as the floret.
13. Floret shape: terete to fusiform = 0 (Fig. 5A–G); obconical = 1 (Cialdella & Arriaga, 1998, fig. 8B, D); obovoid to globose = 2 (Fig. 5H); lens-shaped = 3 (Cialdella & Arriaga, 1998: fig. 10C, D). Floret shape varies among species of *Piptochaetium*, being terete, fusiform, obconical, obovoid, or lens-shaped. *Nassella* presents terete, obovoid, or lens-shaped florets, while in *Hesperostipa* florets are always terete.
14. Lateral compression of the floret: absent or slightly compressed = 0 (Fig. 5A–H); conspicuously compressed = 1 (Cialdella & Arriaga, 1998: figs. 9C, 10C, D). This character is variable among species of *Piptochaetium* and *Nassella*, while in *Hesperostipa* the florets are never laterally compressed.
15. Lemma pubescence: absent = 0 (Figs. 1A, 5H); present = 1 (Figs. 1B, 5G).
16. Papillae of the lemma: absent = 0; present = 1 (Cialdella & Arriaga, 1998: figs. 2D, 10C). Papillae are found in a few species within *Piptochaetium* and *Nassella*, but are always absent in *Hesperostipa*.
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